

CLASSIFICATION OF THE HELICINIDAE: REVIEW OF MORPHOLOGICAL CHARACTERISTICS BASED ON A REVISION OF THE COSTA RICAN SPECIES AND APPLICATION TO THE ARRANGEMENT OF THE CENTRAL AMERICAN MAINLAND TAXA (MOLLUSCA: GASTROPODA: NERITOPSINA)

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ABSTRACT

The present study combines a taxonomical revision of the poorly known Costa Rican Helicinidae, with a detailed investigation of certain morphological structures with respect to their relevance for systematics, culminating in a discussion of the arrangement of the Central American mainland species.

The revision of the Costa Rican species is based on the examination of nearly all type material, coupled with extensive field work and investigations of the collections of the Instituto Nacional de Biodiversidad de Costa Rica and the Florida Museum of Natural History, Gainesville, along with perusal of additional historical material. With minor exceptions, all these species were investigated with respect to the features of shell, operculum, surface sculpture of embryonic shell and teleoconch, internal shell structures, radula, and female reproductive system. In addition, analyses of morphometry and sexual dimorphism were carried out. Faced with a limited amount of material, it became necessary to develop a new preparation method to separate the soft body from the shell without damaging either.

For the higher classification and comparative analysis of the different morphological characteristics, similar examinations emphasizing formerly poorly studied or neglected characteristics, such as embryonic shell and female reproductive system, were carried out for 17 additional species representing the most important related Central American supraspecific taxa using their type species when available. For taxa with inaccessible material, data from the available literature were critically incorporated.

For Costa Rica, 15 species were recognized, among them seven new species, partially published in Richling (2001) – *Helicina echandiensis*, *H. talamancensis*, *H. monteverdensis*, *H. chiquitica*, *H. escondida*, *Alcacia (Microalcacia) hojarasca*, and *A. (M.) boeckeleri* – and two new subspecies – *H. punctisulcata cuericiensis*, and *H. beatrix riopejensis*. Other previously subspecifically separated taxa (*H. funcki costaricensis* Wagner, 1905; *H. tenuis pittieri* Wagner, 1910) were shown to fall within the range of intraspecific variability. Records of the Guatemalan and Mexican species *Helicina oweniana* L. Pfeiffer, 1849, and subspecies, *H. amoena* L. Pfeiffer, 1849, as well as those of *H. fragilis* Morelet, 1851, were proven to be based on faulty identifications and were therefore excluded from the Costa Rican fauna. This fact, together with the recognition of the several new species, shows that the faunal composition of Costa Rica is much more distinct from that of the northern areas than previously assumed. The transitional zone of Nicaragua, however, still remains widely uninvestigated. Only *Helicina tenuis* L. Pfeiffer, 1849, being ecologically very tolerant, *Lucidella lirata* (L. Pfeiffer, 1847), and *Pyrgodomus microdinus* (Morelet, 1851) are widespread, extending from Mexico to Costa Rica, perhaps even farther south. The distribution of the typical Costa Rican species follows the topographical subdivision created by the Central Cordilleras, along with its corresponding effects on the climate.

Contrary to former assumptions, certain features of the female reproductive system proved very useful for the classification of the Helicinidae. For the first time, monaulic conditions have been recognized for *Helicina* and *Eutrochatella*, necessitating the correction of previous descriptions in this respect. Furthermore, the monaulic or diallic state is characteristic of the genera and is paralleled by consistent changes in the embryonic shell struc-

ture. Because primitive members of the Helicinidae possess a diaulic system, the monaulic condition is regarded as the derived state. The Central American genera *Helicina*, *Alcacia*, *Eutrochatella*, *Lucidella* and *Schasicheila* were properly distinguished and described by this, as well as by other differences in the female reproductive system. The anatomies of the type species of *Helicina* and *Alcacia* were examined for the first time, and earlier descriptions of *Eutrochatella* and *Lucidella* were corrected in major points. On the basis of this new evidence, the assignment of traditional subgeneric units of *Helicina* and *Alcacia*, previously based mainly on vague radula and shell characteristics, was especially reassessed. The subgenera *Sericea* and *Analcacia* were transferred to *Helicina*, as well as the mainland land species summarized under the preoccupied taxon "*Gemma*". *Tristramia*, *Oxyrhombus*, *Pseudoligyra*, *Oligyra*, *Succincta*, "*Cinctella*" [also preoccupied] and *Punctisulcata* were confirmed in their association with *Helicina*. Due to its monaulic condition, the former genus *Ceochasma* is reduced to a subgenus of *Helicina*. In addition, exemplary non-type Antillean species were studied, including *Helicina jamaicensis* Sowerby, 1841, which had to be shifted to *Alcacia* s.l., and *Alcacia* (*Analcacia*) *platychila* (von Mühlfeldt, 1816), which is now assigned to *Helicina* s.s. On one hand, the new arrangement excludes *Alcacia* as previously known from the Central American mainland, but, on the other hand, examination of the newly discovered Costa Rican species *Helicina hojarasca* and *H. boeckeleri* required the establishment of a new subgenus of *Alcacia*, *Microalcacia* n. subgen. on the mainland, based mainly on the features of the female reproductive system and embryonic shell structure. The occurrence of *Alcacia* with only a few diminutive species on the mainland of Central America corresponds to the distribution of the genera *Eutrochatella*/*Pyrgodomus* and *Lucidella*.

The Central American mainland species of *Helicina* seem to show a closer relationship among each other than to the northern South American subgenera *Analcacia* and *Sericea*. The Brazilian taxon *Angulata*, previously a subgroup of *Helicina*, deviates remarkably in embryonic shell structure and shows differences in anatomy that still require final confirmation, and it thus deserves recognition as a separate genus.

Contrary to the well-supported differentiation at the generic level, the attempt to characterize subgroups of the Central American mainland species of *Helicina* has been only partially successful. Certain similarities in teleoconch surface structure, relative development of the accessory structures of the female reproductive system, and the degree of sexual dimorphism become obvious and are discussed to some extent, but intermediate characteristics complicate a satisfactory solution. Besides *Ceochasma*, three Central American mainland subgenera are recognized: *Oligyra*, *Tristramia* most closely resembling *Helicina* s.s., and "*Gemma*". The latter preoccupied name is tentatively retained, because the proposal of a new name seems inappropriate at this stage.

Investigation of the morphological features other than the embryonic shell sculpture and the female reproductive system revealed the following additional results, mainly based on the Costa Rican species of *Helicina*:

Characteristics of teleoconch, operculum, and radula, previously regarded as substantial for classification, were repeatedly demonstrated to be subject to convergent development, thus limiting their value for systematics. Different examples are given, such as the T-shaped lateral of the radula or periostracal hairs, and further evidence is provided by the necessary re-arrangements outlined above. Nevertheless, these features play a supplementary or supporting role.

The mantle pigmentation of arboreal Helicinidae is closely related to the transparency of the shell and functionally replaces shell color in thin shells. The physiological possibility of an obviously adaptable mantle pigmentation could provide the opportunity for survival with thin, transparent shells as adaptation to the limited availability of calcium carbonate. Whereas varying and patterned mantle color are characteristic for arboreal thin-shelled species, the color of the head and foot is seldom species specific.

Size differences of the embryonic shell have not previously been studied for Helicinidae. Embryonic shell size is shown to increase with the shell size within a group of related species and also altitude within different populations of a species. Furthermore, it may show

a certain species specificity. Preliminary data on *Lucidella* and *Eutrochatella/Pyrgodomus* suggest a consistently smaller embryonic shell size than in *Helicina* or *Alcadia*.

Internal shell structures – axial cleft and muscle attachments – seem characteristic for certain systematic units, for example, *Lucidella* and *Schasicheila*. The length of the axial cleft is confirmed to be constant within a species, but, contrary to former assumption, it is not related to the whorl count.

The data on sexual dimorphism given in this study represent the most comprehensive approach to date to analyze this phenomenon for Helicinidae. The sexual dimorphism may manifest itself in differences in volume, a male's size being only about 62–70% of that of the female's, but formerly assumed deviations in shape could not be proved to be of significance for species of *Helicina*. A certain value for the degree of differences in uncovering systematic affinities is indicated.

Keywords: Helicinidae, Costa Rica, Central America, classification, reproductive system, radula, embryonic shell, new species.

RESUMEN

El presente estudio combina una revisión de los poco conocidos helicinidos de Costa Rica con un análisis detallado de varias estructuras morfológicas y su utilización para resolver preguntas sistemáticas. Con base en esto se discute a profundidad la clasificación de las especies continentales de Centroamérica.

La revisión de las especies costarricenses se basa en un exhaustivo trabajo de campo, en el análisis de casi todo el material tipo, de las colecciones del Instituto Nacional de Biodiversidad de Costa Rica y del Museo de Historia Natural de Gainesville, así como de material histórico. Con pocas excepciones se estudiaron para todas las especies los caracteres de la concha, del opérculo, de la estructura superficial de la concha embrionica, así como de la teleoconcha, estructuras internas de la concha, la rádula, y el tracto reproductor femenino. También se efectuaron estudios sobre morfometría y dimorfismo sexual. Considerando la escasez de material, para efectuar un estudio a gran envergadura, fue necesario desarrollar una metodología de disección para separar el cuerpo blando de la concha sin ningún detrimento.

Para efectuar una clasificación más amplia y una comparación de las diferentes estructuras morfológicas se tomaron los mismos datos de otras 17 especies, que representan los taxa supraespecíficos emparentados más importantes de Centroamérica.

Énfasis se puso en las estructuras poco estudiadas hasta ahora como la concha embrionica y el tracto reproductor femenino. Hasta donde se pudo se trabajo con material de especies que corresponden a los tipo. En donde no se pudo obtener material anatómico para estudiar se interpretaron cuidadosamente los datos de la literatura.

Para Costa Rica se determinaron 15 especies, entre las cuales siete son nuevas, y en parte publicadas en Richling (2001) – *Helicina echandiensis*, *H. talamancensis*, *H. montevertensis*, *H. chiquitica*, *H. escondida*, *Alcadia (Microalcadia) hojarasca* y *A. (M.) boeckeleri*, además dos nuevas subespecies *H. punctisulcata cuericiensis* y *H. beatrix riopejensis*. Los taxa subespecíficos, hasta ahora separados, *H. funcki costaricensis* Wagner, 1905, y *H. tenuis pittieri* Wagner, 1910, caen dentro de la variación intraespecífica. La presencia de las especies mejicanas y guatemaltécas *Helicina oweniana* L. Pfeiffer, 1849 con sus subespecies, *H. amoena* L. Pfeiffer, 1849 y *H. fragilis* Morelet, 1851 no fue confirmada ya que el material estaba mal identificado y por esto se las elimina del listado faunístico de Costa Rica. Debido a este hecho y al descubrimiento de algunas nuevas especies se puede distinguir la fauna de Costa Rica más claramente de otras regiones más al norte de lo que se suponía hasta ahora. Nicaragua que es el territorio de transición está casi inexplorado. Solamente las especies *Helicina tenuis* L. Pfeiffer, 1849, que presenta una gran tolerancia ecológica, así como *Lucidella lirata* (L. Pfeiffer, 1847) y *Pyrgodomus microdinus* (Morelet, 1851) se distribuyen desde México hasta Costa Rica y también más hacia el sur. La distribución de las especies típicas costarricenses sigue la subdivisión topográfica de las cordilleras centrales y sus efectos correspondientes al clima.

Contrario a suposiciones anteriores, se pudo demostrar que los caracteres del tracto reproductor femenino son muy útiles en la clasificación de los helicínidos. Por primera vez se pudieron reconocer condiciones monáulicas en *Helicina* y *Eutrochatella* por lo que descripciones previas se deben corregir a este respecto. Además la condición monáulica o diáulica son característicos para cada género y paralelamente hay cambios consistentes en la estructura de la concha embrionica. Ya que los miembros primitivos de los helicínidos poseen un sistema diáulico, la condición monáulica es considerada como derivada. Los géneros centroamericanos *Helicina*, *Alcadia*, *Eutrochatella*, *Lucidella* y *Schasicheila* se distinguen claramente y son descritos por estos y otros caracteres de la genitalia femenina. La anatomía de las especies tipo de *Helicina* y *Alcadia* se estudiaron por primera vez y las descripciones anteriores de *Eutrochatella* y *Lucidella* se debieron corregir en varios puntos importantes. Sobre esta nueva base, especialmente la asignación de las tradicionales unidades subgenéricas de *Helicina* y *Alcadia*, que estaban previamente basadas en caracteres vagos de la rádula y la concha, fueron reordenaron. Los subgéneros *Sericea* y *Analcadia* se transfirieron a *Helicina* así como las especies continentales comprendidas bajo el taxón preocupado "*Gemma*". La pertenencia a *Helicina* de *Tristamia*, *Oxyrhombus*, *Pseudoligyra*, *Oligyra*, *Succincta*, "*Cinctella*" (también preocupada) y *Punctisulcata* se confirma. Debido al tracto genital monáulico, el género *Ceochasma* se ordena como subgénero de *Helicina*. Especies de la Antillas solo se estudiaron ejemplarmente, *Helicina jamaicensis* Sowerby, 1841, se incluyó dentro de *Alcadia* s.l. y *Alcadia* (*Analcadia*) *platychila* (von Mühlfeldt, 1816) se le asigna a *Helicina* s.s. Por una parte estos datos excluyen al género *Alcadia* del continente centroamericano, por otra parte el análisis de las nuevas especies costarricenses encontradas de *Helicina hojarasca* y *H. boeckeleri* requirieron la instauración del subgénero *Alcadia*, *Microalcadia* n. subgen., para el continente basandose mayormente en los caracteres del tracto reproductor femenino y de la concha embrionica. La presencia de *Alcadia* con solo unas cuantas pequeñas especies en el continente corresponde a la distribución de *Eutrochatella*/ *Pyrgodomus* y *Lucidella*.

Las especies continentales centroamericanas de *Helicina* parecen estar más emparentadas entre si, que con los subgéneros *Analcadia* y *Sericea* del norte de Suramérica. El taxón brasilero *Angulata*, subordinado a *Helicina*, posee una estructura de la concha embrionica claramente distinta y diferencias anatómicas todavia por corroborar, por esto se le considera como un género aparte.

Contraria a la clara diferenciación a nivel genérico, el intento de agrupar las especies continentales de *Helicina* ha sido solo en parte exitoso. Algunas similitudes en la estructura superficial de la teleoconcha, el desarrollo relativo de las estructuras accesorias del aparato reproductor femenino, y el grado de dimorfismo sexual son obios y se discuten en parte, pero estadios intermedios complican la solución satisfactoria de este problema. Además de *Ceochasma*, se reconocen tres subgéneros centroamericanos continentales: *Oligyra*, *Tristamia* muy parecido a *Helicina* s.s. y "*Gemma*". Este último está preocupado pero se le retiene tentativamente, ya que proponer un nuevo nombre a este nivel no se considera apropiado.

El estudio de otros caracteres morfológicos diferentes a la estructura de la concha embrionica y del aparato reproductivo femenino revelan los siguientes resultados adicionales, basados especialmente en las especies costarricenses de *Helicina*:

Se demostró repetidamente que las características de la teleoconcha, opérculo y rádula, previamente considerados fundamentales para la clasificación, son objeto de desarrollos convergentes, limitando así su valor sistemático. Diferentes ejemplos son dados como el diente lateral en forma T de la rádula o los filamentos del perióstraco. Evidencia adicional es dada en la reorganización requerida mencionada anteriormente. Sin embargo estos caracteres juegan un papel suplementario o de soporte.

La pigmentación del manto de los helicínidos arbóreos está fuertemente relacionada con la transparencia de la concha y reemplaza funcionalmente la coloración de la concha en conchas delgadas. La posibilidad fisiológica de la pigmentación del manto se considera como una adaptación obia que permite la supervivencia con conchas delgadas, en ambientes con poco calcio. Mientras que los patrones de coloración del manto son

característicos para las especies arbóreas con conchas delgadas, la coloración de la cabeza y el pie son raramente característicos a nivel de especie.

Las diferencias del tamaño de la protocóncha no se habían estudiado previamente en los helicínidos. Se demuestra que el tamaño de la concha embrionica aumenta con el tamaño de la concha en un grupo de especies relacionadas y con la altitud de la localidad de diferentes poblaciones de una especie. En algunos casos el tamaño de la concha embrionica puede ser característico para una especie. Primeros datos de *Lucidella* y *Eutrochatella*/*Pyrgodomus* muestran constantemente una concha embrionica más pequeña que en *Helicina* o *Alcadia*.

Las estructuras internas de la concha – apertura axial e inserción de los músculos – parecen ser característicos para algunas unidades sistemáticas, e. j. *Lucidella* y *Schasicella*. La longitud de la apertura axial es constante dentro de las especies, pero, contrariamente a lo que se suponía, no está relacionada con el número de vueltas.

Los datos sobre dimorfismo sexual dados en este trabajo representan la aproximación más amplia hasta la fecha para analizar este fenómeno en los helicínidos. Este estudio muestra diferencias significativas en el volumen, en donde los machos en casos extremos solamente alcanzan aproximadamente entre el 62 y el 70% del tamaño de las hembras. Contrariamente a las suposiciones anteriores no se pudieron comprobar diferentes formas en el género *Helicina*. El grado de dimorfismo sexual parece tener también valor al determinar las relaciones de parentesco.

INTRODUCTION

The Helicinidae and a few related families belonging to the Neritopsina represent the earliest branch of gastropods evolved to terrestrial existence from as-yet unknown diotocardian marine ancestors. Their recent distribution encompasses two main regions – the subtropical and tropical zones of North and South America and the Indopacific and Pacific islands and small areas of the Asian and Australian continents. A particular high diversity has developed on the Caribbean Islands and on the Philippines. The family is comprised of approximately 550 species, of which a little more than half occur in the New World. Most species are small, with only the largest representatives reaching nearly 3 cm.

Early classifications of the Helicinidae were based on shell characters only (e.g., L. Pfeiffer, 1850–1853). Later, Wagner (1907–1911) provided the still most extensive, but much criticized (e.g., Fulton, 1915; Solem, 1959: 166–167) monograph on the family worldwide, incorporating features of the operculum for his systematic arrangement. At about the same time, a very detailed, comprehensive anatomical investigation of several New and Old World species of different genera, including histology, was published by Bourne (1911). His study demonstrated a considerable uniformity of the morphological structures within the Helicinidae, indicating their very limited value for revealing system-

atic affinities, especially with respect to the reproductive system. In conclusion, Bourne (1911) favored radular characteristics as the safest feature for a classification. Baker (1922a, 1923) followed this concept to clarify the relationships of the American mainland taxa (United States to northern South America) and nomenclaturally corrected, modified and consolidated the system of Wagner (1907–1911) through radula characteristics that were believed to provide systematically relevant information. Subsequent anatomical studies on the same group of species with emphasis on the reproductive system (Baker, 1926, 1928) did not allow similar conclusions to be drawn due to the uniformity of the structures and the limited material. Later authors interpreted the results in the sense of Bourne (1911) and stated that the "... general uniformity of the genitalia of the Helicinidae makes them useless for diagnostic purposes" (Boss & Jacobson, 1974: 6). The radula characteristics were partly accepted, but other authors questioned their value for certain taxonomical units (Rehder, 1966; Boss & Jacobson, 1973). The most recent contribution to systematic issues of Helicinidae by Thompson (1982) highlights the conservative character of embryonic shell sculptures as a criterion for determining relationships, but its further application was beyond the scope of his study on a species-group from the West Indies. The few publications dealing with the classification of the Australasian and Pacific

species are based on shell structures or vague differences in the radula, respectively. In conclusion, it can be stated that the systematics within the Helicinidae still remain controversial, and due to the fact that the studies of the different structures were mostly based on different taxa, they are not comparable and any interpretation is, at the very least, partially questionable.

Faced with the absence of a detailed investigation of the applicability of different features to reveal affinities within the Helicinidae and a comparison of all these characteristics for one and the same group of species, this study tries to bridge this gap. Furthermore, preliminary studies on the female reproductive system of a Costa Rican species showed deviations from the previous results, rendering these organs more informative than described above. Therefore, the present study intends to investigate several morphological characters for their value in determining relationships on the species level (rather highly adaptable) and in higher systematics (rather conservative). The chosen characteristics will encompass widely applied aspects, such as shell in general, operculum and radula, but will also focus on less investigated or neglected structures, such as teleoconch surface structure, embryonic shell, internal shell structures, female reproductive system, and the phenomenon of sexual dimorphism.

Because single structures can only partially be assessed in their possible adaptability by their complexity and functionality alone, they also have to be discussed within the context of the best possible, well-founded synthesis of all possible characteristics, that is, the proposed classification. Therefore, the analysis of structures is based on revision of one group of closely related species (species level) and study of other related supraspecific taxa (higher systematics, e.g., type species of respective genera and subgenera). This will result in a new proposal for the classification of the taxa studied, which is compared with possibly deviating previous concepts.

This study will be based on the Costa Rican representatives of Helicinidae, which encompass a reasonable number of species for detailed analysis. According to Wagner (1907–1911) and Baker (1922a, 1926), most of the species belong to one or two genera, *Helicina* or *Helicina* and *Alcadia*. Single species of *Lucidella* and *Pyrgodomus* represent relatives of genera with otherwise Antillean distributions. Two newly discovered species

(Richling, 2001) still await proper classification. Thus, a fairly wide scope of systematic units is included and, with respect to the Costa Rican species, part of the Central American mainland fauna has been chosen for which the most data for comparison, mainly from the works of Baker, are available.

The focus on the Costa Rican species provided the opportunity to carry out a revision of the Helicinidae of a poorly investigated area as well. Because von Martens (1901: xii) still has characterized the molluscan fauna as "one of the best known within Central America", a few scattered publications in the 1930s (e.g., Pilsbry) remained in complete neglect until recently, when the growing interest in tropical biodiversity, spearheaded by the foundation and work of the Instituto Nacional de Biodiversidad de Costa Rica (INBio), resulted in a new approach. The cooperation with the Zaidett Barrientos of the Malacology Section of INBio in providing access to the comprehensive collection of national molluscs greatly ameliorated the disadvantage of the unfavorable geological conditions of Costa Rica for collecting terrestrial snails which result in extremely low abundances and therefore present practical difficulties for obtaining sufficiently large numbers of specimens for certain aspects of the study.

MATERIALS AND METHODS

Area of Investigation

Costa Rica is situated in southern Central America adjacent to Nicaragua to the north and Panama to the south (about 8° to 11°15'N). Located between the Pacific Ocean and the Caribbean Sea, small area of just 51,100 square kilometers rises up to 3,820 m above sea level. The central mountain chain, northwest to southeast in orientation, separates a larger Caribbean from a hilly Pacific plain. The mountains are subdivided into the northern Cordillera de Guanacaste, the Cordillera de Tilarán, and the Cordillera Central, a chain of volcanoes, some of them still active, and the southern Cordillera de Talamanca which has been uplifted as a result of the subduction of the Cocos Ridge (Fig. 1).

The climate is characterized by a dry and a rainy season, with the dry season lasting from about December to May. Whereas the northwestern and central parts of the country really experience a dry period, the southern Pacific

side as well as the Caribbean side always have humid conditions. This is reflected in the variation of the vegetation, the tropical dry forest only being found in the northwestern area in the transition to the Península de Nicoya. The vegetation of the remaining part of the country is classified as moist, wet or rain forest (Tosi, 1969), with the humidity mainly increasing with the altitude (Fig. 2). The distribution of the annual precipitation is given in Fig. 3.

Materials

Fieldwork:

COSTA RICA. The field work was carried out on five visits of about 4 to 9 weeks each to

Costa Rica between 1998 and 2001. With one exception during the rainy season of July to September, the field trips were carried out during the dry season in February and March. Several localities scattered around the country were investigated for distributional data. Selected areas were visited several times in order to gather sufficient material of certain populations for comparative studies, because their abundance in the tropical rain forests is very low. Due to the arboreal life-style of most of the Costa Rican species, manual searches had to be conducted. The detailed material and localities are listed under each species. Main collecting sites are shown on the general map (Fig. 1).

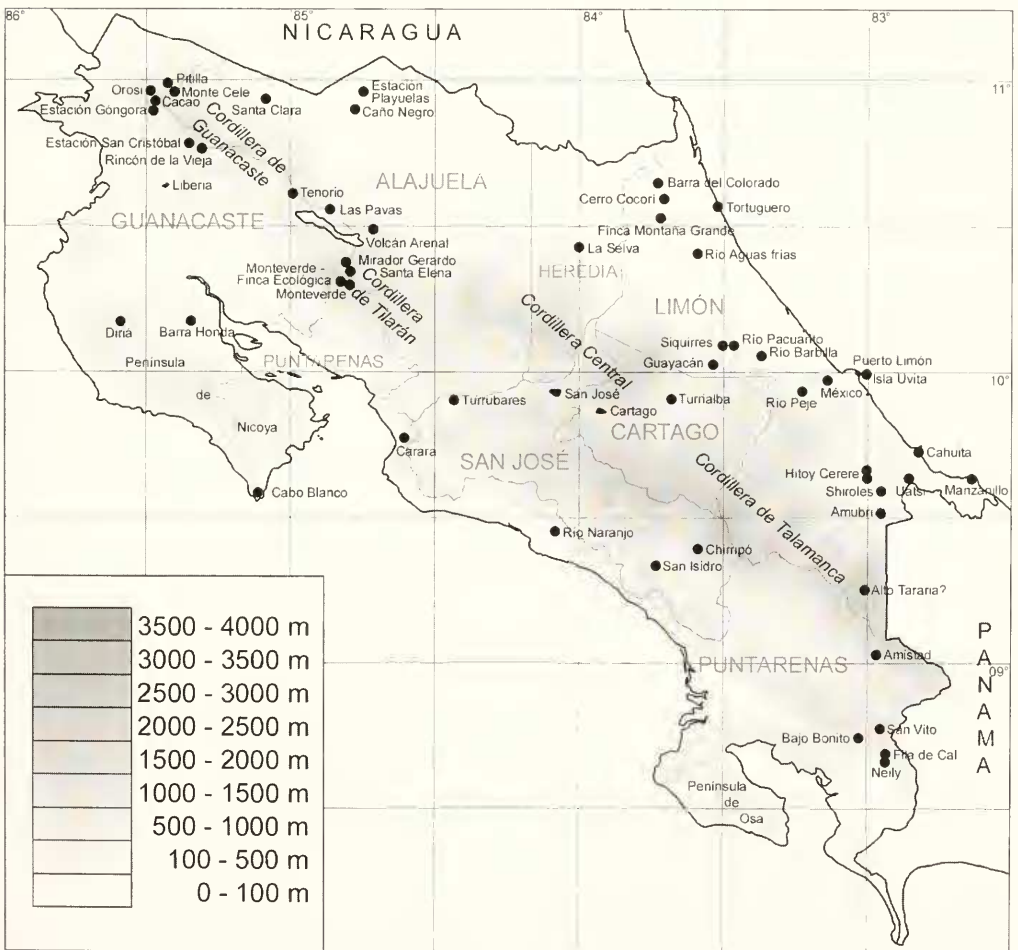


FIG. 1. Map of Costa Rica, including the most important collecting sites, the central mountain chains, and the provinces.

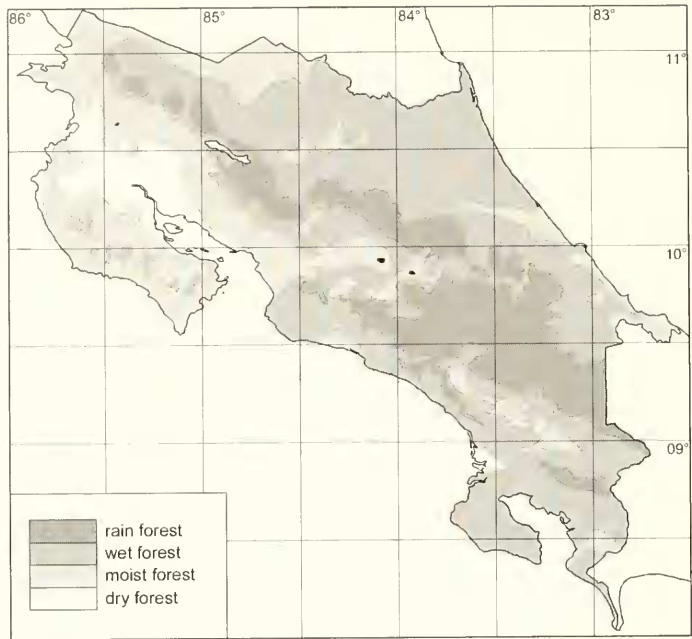


FIG. 2. Vegetation zones of Costa Rica (based on Tosi, 1969).

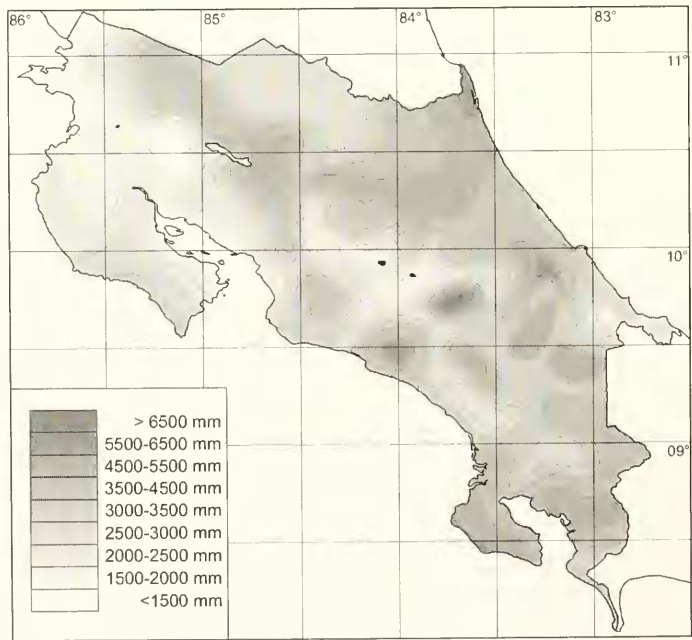


FIG. 3. Annual precipitation in Costa Rica [mm/year] (based on Ministerio de Agricultura y Ganaderia & Instituto Meteorologico Nacional, 1985).

JAMAICA/UNITED STATES. Because the type species of the most important Central American genera (*Helicina*, *Alcadia*, *Lucidella*, *Eutrochatella*) occur in Jamaica, and preserved material was not available in collections, supplementary research was carried out during two weeks in May/June 2001. Specimens of *Helicina orbiculata* (Say, 1818) were collected in Gainesville, Florida, in May 2001.

Museum Collections: Material of the following institutions has been studied, subsequently only the abbreviations will be used:

ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia, USA (Dr. Gary Rosenberg, Dr. Igor Muratov)
APHIS-PPQ USDA	Malacological Collection of United States Department of Agriculture, Philadelphia, USA (Dr. David G. Robinson)
BMNH	The Natural History Museum, London (formerly British Museum, Natural History), Great Britain (Dr. Fred Naggs, Richard Williams)
HNC	Haus der Natur Cismar, Germany (Dr. Vollrath Wiese)
INBio	Instituto Nacional de Biodiversidad de Costa Rica, Santo Domingo, Costa Rica (Dr. Zaidett Barrientos)
IR	Material collected by Ira Richling, partially deposited as vouchers at INBio, otherwise accessible through the collection of the HNC; a few of the numbers refer to field observations only
MHNN	Musée d'Histoire Naturelle, Neuchâtel, Switzerland (Dr. Jean-Paul Haenni)
MIZ	Museum and Institute of Zoology of the Polish Academy of Sciences in Warszawa, Poland (Prof. Dr. Adolf Riedel)
NMBE	Naturhistorisches Museum Bern, Bern, Swiss (Dr. Margret Gosteli)
RMNH	Nationaal Natuurhistorisch Museum, Leiden (formerly Rijksmuseum van Natuurlijke Historie), The Netherlands (Wim Maassen)
SMF	Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt a.M., Germany (Dr. Ronald Janssen)

UF	Florida Museum of Natural History, Gainesville, USA (Dr. Fred G. Thompson, John Slapcinsky)
USNM	United States National Museum, Washington, D.C., USA (Dr. Robert Hershler)
ZMB	Museum für Naturkunde, Humboldt-Universität, Berlin, Germany (formerly Zoological Museum Berlin) (Dr. Matthias Glaubrecht)
ZMH	Zoologisches Museum, Universität Hamburg, Hamburg, Germany (Dr. Bernhard Hausdorf)

INBio: Within a context of considerable recent efforts towards an inventory of the biodiversity of Costa Rica, the institute houses a very extensive collection of molluscs. All available specimens of Helicinidae from this material were studied, partially during personal visits in Costa Rica, partially by loans to Germany.

UF: This institution houses probably one of the most comprehensive collections of Central American terrestrial molluscs. During a two-week visit, about 1,100 lots of Helicinidae were studied with the emphasis on the mainland species yielding considerable distributional data.

ZMB/MHNN: The only important historical collections in Costa Rica were made by the Swiss naturalists Bivolley and Pittier at the end of 19th century. Their material ended up in different collections, parts of it in the ZMB and MHNN respectively, other parts remained in the Museo Nacional in San José, Costa Rica (see under *Helicina pitaleensis*). The ZMB collection was visited personally, whereas material in the MHNN was searched for by J.-P. Haenni, Neuchâtel, and kindly loaned to the author. According to J.-P. Haenni, an up-to-date catalogue of the mollusc collection does not exist and the materials of Pittier and Bivolley are scattered throughout the collection, which has never actually been catalogued and which was moved in the past, and it is possible that some of the material has not yet been found. A detailed list of material studied is given under each species.

Locations/Maps: During the field work, coordinates of the localities were registered using the Global Positioning System (Magellan GPS 3000) whenever possible, otherwise

they were taken from maps in 1:50,000 scale produced by the Instituto Geográfico Nacional, San José, Costa Rica, in different editions, but all based on data from between 1961 and 1966. The staff of INBio uses the same maps. All Costa Rican records from literature or other sources without exact data were localized as accurately as possible and coordinates were estimated based on the map: Los Parques Nacionales y otras áreas protegidas de Costa Rica. – Fundación Neotrópica, San José, 1993, I Reimpresión 1995. Information on some historical collecting sites was provided by Zaidett Barrientos and Maribel Zuñiga, INBio. All further explanations that were subsequently added are given in brackets.

The map of Costa Rica used throughout this study is based on: Costa Rica. Mapa físico-político 1:500.000 – Instituto Geográfico Nacional, San José, edition 1987.

Methods

Measurements: The following linear measurements (Fig. 4) were used, when measurements of single species given, the following sequence is given, separated by “/” (unless otherwise stated):

height
major diameter
greatest diameter
minor diameter
expansion of outer lip

height of last whorl
height of columellar axis

Because some helicininid species display variation in the development of the outer lip which mainly influences the measure of the greater diameter, measurement of “major diameter” has been introduced. This measurement was taken just behind the reflection of the outer lip (Fig. 4). For the height, this modification was not applied, because it is not affected as much and is furthermore not uniformly practicable.

The greatest diameter is usually included only in measurements given for single specimens to comply with traditional measurements.

Measurements were taken with a micrometer gauged on 0.01 mm scale. In view of the deviation shown below that were minimized by personal experience, values given to characterize single specimens were rounded to a 0.1 mm scale. Deviations are mainly due to effects of an imperfect perpendicular orientation of the shell with respect to the measuring axis, a problem that can be minimized with experience if the same person carries out the measurements. However, errors probably cannot be excluded in globular shells, but their range is tolerable. To check the average deviations, three shells of different shapes were measured the different times and the mean value, the standard deviation and absolute deviations were analyzed (Table 1).

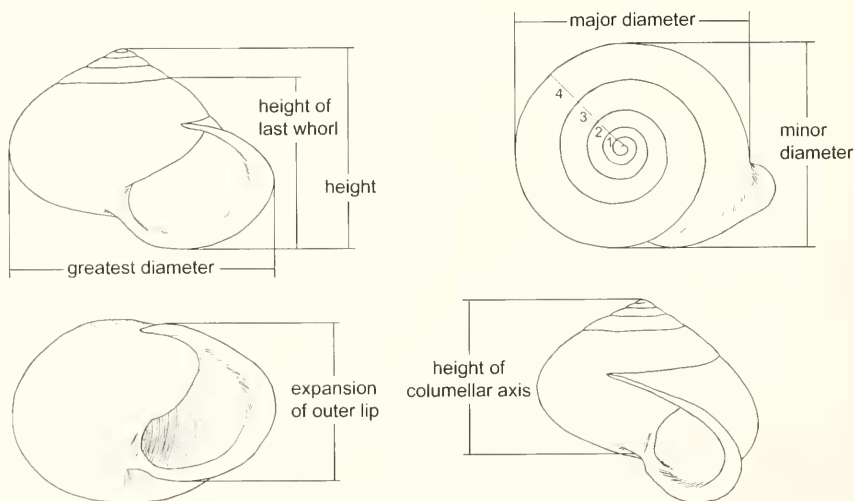


FIG. 4. Measurements and counting of postembryonic whorls.

TABLE 1. Analysis of deviations in measuring procedure of Helicinidae for three individuals of different species, all measurements in mm, maj./min. diam. = major/minor diameter, col. axis = columellar axis.

	<i>Helicina beatrix confusa</i> lot IR 1113					<i>Helicina funcki</i> lot IR 1555					<i>Helicina gemma</i> lot IR 1460				
	Mean value	Standard deviation	Min	Max	Number	Mean value	Standard deviation	Min	Max	Number	Mean value	Standard deviation	Min	Max	Number
Height	8.30	0.02	8.27	8.33	10	10.78	0.04	10.72	10.85	10	6.61	0.03	6.57	6.66	10
Maj. diam.	7.38	0.03	7.34	7.43	10	12.33	0.09	12.18	12.53	10	6.13	0.01	6.12	6.15	10
Greatest diameter	7.75	0.03	7.70	7.81	10	13.49	0.03	13.44	13.56	10	6.47	0.01	6.43	6.49	10
Min. diam.	7.05	0.02	7.02	7.08	10	11.06	0.02	11.03	11.10	10	5.69	0.01	5.67	5.71	10
Outer lip	4.80	0.03	4.74	4.85	10	7.81	0.02	7.78	7.84	10	3.86	0.02	3.82	3.90	10
Last whorl	6.14	0.03	6.10	6.18	10	8.87	0.04	8.78	8.94	10	4.91	0.05	4.83	4.98	10
Col. axis	6.53	0.03	6.46	6.60	10	8.17	0.05	8.09	8.36	10	5.13	0.03	5.08	5.22	10

In addition to the linear measurements, the weight and volume of empty shells were analyzed. Sartorius scales (scale 0.001 g) were used. The volume was measured as the difference of weight of the shell filled with distilled water and the weight of the empty shell. To obtain comparable data, shells were always filled until the water showed a plain surface in the aperture. In the weight measurements, the hole caused by the preparation procedure did not influence the results, because the wall at the beginning of the last whorl is thin and the amount of material removed was below the scale of resolution.

Except for the specimens studied with the SEM, the diameter of the embryonic shell was measured under a stereomicroscope (scale 20 μm). Otherwise, measurements were taken from photographs, which are much more exact. Whorls were counted according to Fig. 4.

Fixation: The preservation of the live collected material was carried out in two ways:

(1) Collections until 1999: Specimens were relaxed in water for several hours and subsequently transferred to isopropanol (about 80%).

This method has disadvantages: It is difficult to find the right time to stop the relaxation process, because it depends on so many factors, such as specimen size, water volume and temperature. Under the conditions of field work and travel by bus, it is difficult to carry out lengthy procedures. Furthermore, the shocks received during transport also influence timing. As a result, the specimens may be badly preserved or contracted. In case they close their opercula again, there remains the risk that the alcohol will not penetrate into the shell.

Beginning in 2000, I developed the new method to remove the body from its shell described below, which allowed another preservation method mitigating these disadvantages.

(2) Collections after 1999: Specimens were removed from the shell alive and immediately dropped in isopropanol.

It has the advantage that specimens can be preserved immediately and with a constant result. The problem of the closure of the operculum becomes irrelevant. If a relaxation is required for subsequent investigations, the body can still be dropped in water or other solutions and will be anaesthetized

much faster due to the greater unprotected surface for medium exchange. For the present study and due to the need of a fast working method, a relaxation process has usually not been applied, because retractions are limited to the foot and the two portions of the retractor muscle and do not greatly affect other organs.

Preparation and Storage of Material: Against the background of the low abundance of Helicinidae in Costa Rica and the various aims of the study (e.g., aspects of anatomy, sexual dimorphism), two requirements had to be met at the same time: the shell and the animal had to be separated and they had to be kept as intact as possible.

When normally pulling a more or less relaxed animal out of its shell, in most cases the head-foot and the anterior pallial portion will be released, but the remaining part will be torn off within the shell. This is due to the fact that in the Helicinidae, contrary to most other gastropods, by the dissolution of the inner whorls of the shell, the visceral mass forms one large complex, which has a greater diameter than the remaining part of the last whorl or aperture respectively, through which it has to pass. Furthermore, air cannot penetrate to allow the body to be released. Besides the obvious disadvantages, the resulting rupture of the body directly divides the pallial gonoduct at an important section and often makes its study impossible.

In a newly developed method, a small hole is made on the periphery within about the second quarter of the last whorl (Fig. 5, arrow) with a nail file or insect needle of different size, depending on the shell thickness. This can be performed without injury to the animal when applying the method to live individuals. Subsequently, a needle, curved if necessary, is carefully inserted between shell wall and body and the two retractor muscles are detached. Afterwards, the ani-

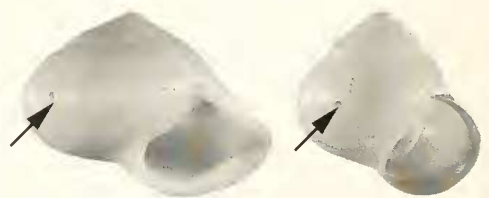


FIG. 5. Hole for removal of the body.

mal can easily be removed by pulling the operculum (live animals) or by a needle inserted in the foot (preserved animals). One must be careful to allow air to enter the hole. Live animals can then be fixed. In preserved specimens, it is usually more complicated during the final removal to avoid the damage described above, because the visceral mass is no longer very flexible or may suffer from poor preservation. By the aid of the needle (through the hole), the visceral mass then has to be squeezed through the remaining part of the last whorl. The success in preserved specimens greatly depends on the shell shape (relation of shape and volume of visceral mass to the diameter of the aperture) and the prior fixation. During the present study, the method seldom failed. In my own material, shells were separated from the bodies in all adult and live collected specimens. They were individually stored, enumerated and labeled.

Sex Determination: The determination of the sex was done by external inspection of the soft body. According to Baker (1926) and personal experience, in most cases and many species a dissection is not necessary. Females are recognized by the comparatively small lobes of the ovary, widely spaced, regular constrictions of the pallial gonoduct (not in all species), and the dark color of a distinct portion of the distal pallial gonoduct. Males are characterized by the comparable larger lobes of the testis, the absence of the distinct dark color, a very densely lobed apical, and smooth distal part of the pallial gonoduct. In some cases, the shiny white vas deferens may shimmer through the visceral mass. Normally not all these features are visible in one and the same specimen, but each one may be un-

equivocal. It mainly depends on the body pigmentation, the species and the individual development. In ambiguous cases, the specimen was dissected.

Reproductive System: Dissections were made in 70% isopropanol or ethanol. For the investigation of the reproductive system, the mantle cavity was opened along the left side of the intestine, with the latter remaining along the pallial gonoduct. A second cut was made between the pallial gonoduct and the right retractor muscle, along or through the hypobranchial gland up to the apical part of the pallial portion of the reproductive system (Fig. 6).

Histology: The separated female reproductive system was dehydrated through a series of ethanol, transferred to paraffin via acetone (100%) and embedded in paraffin. Serial sectioning was done at 5–7 μ m with a sliding microtome. The tissue was subsequently stained with a sequence of paraldehyde fuchsin solution, nuclear fast red and orange G/ light-green.

Preparation of Shells for SEM: In order to reduce lasting effects to the shell by gold coating, the specimens were usually mounted on aluminum specimen stubs using adhesive conductive tape. Subsequently, they were tightly covered with laboratory film (Parafilm "M[®]"), which adhered to the remaining surface of the adhesive conductive tape. Finally, the embryonic shell or other areas of interest were uncovered and coated. After the SEM investigation the laboratory film can easily be removed and the shell extracted.

Preparation of the Radula: The radula was removed from the buccal mass. It was cleaned

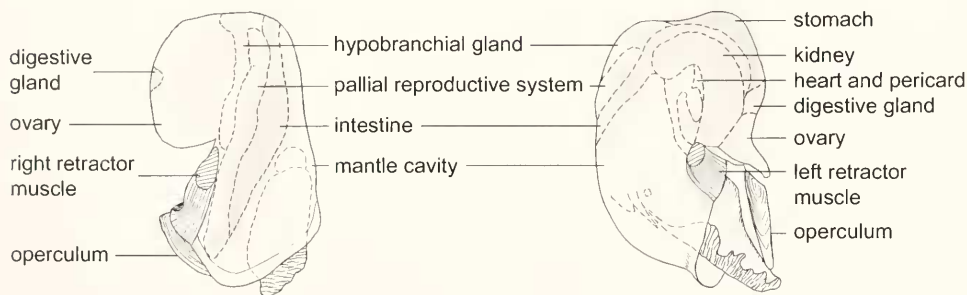


FIG. 6. General anatomy of the Helicinidae.

from remaining tissue in NaOH-solution (1 N) for about 24 h at 50°C. Subsequently the radula ribbon was washed in distilled water several times and dehydrated through a series of ethanol (70%, 80%, 96%, 100%). After the pure alcohol, it was dried and arranged to the final mounting position with the marginal teeth turned up by using preparation needles. Finally, the radula was mounted with conductive carbon cement on the aluminum specimen stubs for SEM examination. Only a few radulae were studied with the light microscope. For light microscopy, the radulae were transferred to the slides directly after removal.

SEM Investigation of Shells and Radulae:

Samples were sputtered with gold for 140 sec by using a BALTEC SCD 050 Sputter Coater. Investigations were carried out with a LEO 420 scanning electron microscope (LEO V 02.04). Radulae had to be studied under low voltage conditions (about 2.5 kV), because the structure of the rhipidogloss radula causes extremely high charge distributions, rendering adequate studies and exposures under high voltage conditions impossible.

Figures: Unless otherwise stated, all drawings, maps and photographs in the study were made by the author. Drawings were made at a LEICA MZ 8 stereomicroscope by the aid of a camera lucida. Except for Figures 140, 228, 249, 257, and all live animals photographed with a 35 mm SLR camera, all shells were digitized with a Sony Digital Still Camera DSC-F505V.

Additional Abbreviations:

ad./ads. – adult/s
coll. – collection
juv./juvs. – juvenile/s
SEM – scanning electron microscope

RESULTS

The results are presented into two parts: (1) Revision of all Costa Rican species of Helicinidae including the investigation of the shell – general aspects, internal structure, surface structure, embryonic shell, morphometry and sexual dimorphism – the radula, the soft body color, the female reproductive system, and data on the habitat and distribution.

(2) The morphological characters of the supraspecific taxa relevant for the classification of the Central American mainland Helicinidae.

GENERAL ASPECTS

The discussion under each species will focus on the species-relevant data. Aspects of the morphological characteristics will be discussed in context with the classification subsequent to the Results, as will some general results for the Costa Rican fauna and the classification of the Helicinidae. The account for each species has the following outline, in which I have here included an overview of the morphological characters.

Literature Records (without heading): All literature records of the respective species are listed. In some cases of questionable determinations, attempts to re-examine the original material were made. Some citations nevertheless remained uncertain, those are marked by a “?”.

Synonymy: For clarity, the synonyms are reiterated from the Literature Records. This includes only synonyms that were proved and accepted during this study.

Original Description: Complete citation of the original description.

Type Material: This exclusively includes the type material of the respective species.

Type Locality: Only the type locality of the respective species is given under this heading.

Type Material of Synonymous Taxa or Similar Species: If necessary for comparison, information on the type material of synonymous taxa or similar species is also provided, because for many Central American taxa adequate figures cannot be found in the literature. For those species, the type locality is given here.

Examined Material: For a better finding of the data of the lots, the material is arranged according to the collections (leg. I. Richling, collection INBio, other sources) and, only secondarily, according to localities (Costa Rica: different provinces; other countries).

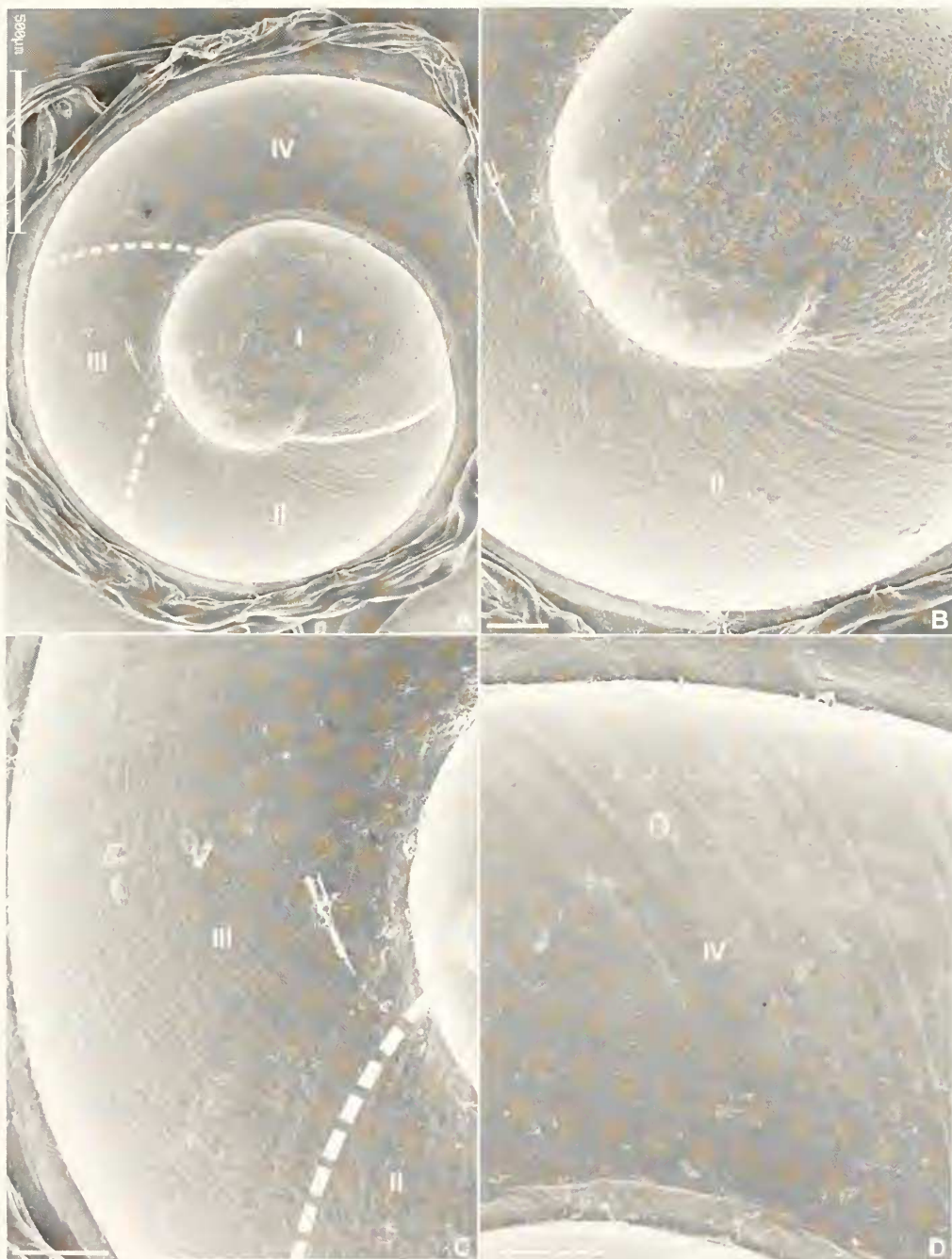


FIG. 7. Changes in shell surface structure exemplary shown for *Helicina gemma*. A. I: Embryonic shell; II: Transitional structure; III: Oblique diverging grooves; IV: Smooth surface with fine growth lines. B. Enlarged view of the transitional structure (section II). C. Pattern of oblique diverging grooves with transformation of section II. D. Enlarged view of the smooth surface with fine growth lines (section IV); scale bars 500 µm (A); 100 µm (B–D).

To shorten the descriptions of the localities and to facilitate the search for the complete locality data mentioned in the text, the following typological convention is used for the Richling and INBio material. In the case of a single locality for lot(s), only a shortened name of the locality is set in italics. In the case of several lots from sublocalities, the entire general description is in italics, followed by a colon; the colon is then followed by further specifications in italics applying to the lots following the second colon. In some cases, there is a further subdivision, such as altitude, given in the same format. Locality data in roman type refer only to the subsequent lot.

Description:

Shell: General description of the species.

Internal Shell Structures: Contrary to most other gastropods, Helicinidae dissolve the inner parts of their shells so completely that only a septum of a certain length subdivides the shell internally. This septum extends from the remains of the columella to the suture of the last whorl. The length of the septum or, referring to the soft body, of the axial cleft is figured here. Additionally, the positions of the attachments of the retractor muscles are shown. In Helicinidae, the columellar muscle is separated in two portions, one attaching somewhere in the umbilical area, the other in the upper part of the shell, often close to the beginning of the axial cleft.

Teleoconch Surface Structure: During growth, the Helicinidae produce different shell surface structures. A possible sequence of different patterns is shown for *Helicina gemma* (Fig. 7) covering the variations among in Costa Rican helicinids.

The embryonic shell (Fig. 7A: I) is sharply distinguished from the teleoconch by a distinct pattern and a more or less clear growth mark. The subsequent part exhibits an irregular, coarse and wrinkled surface ("transitional structure") (Figs. 7A: II, B). It changes continuously with pits elongating to grooves to a pattern consisting of groups of parallel grooves that diverge acutely with other obliquely orientated groups of grooves (Figs. 7A: III, C). The grooves follow two main orientations (this structure will subsequently be referred to as "pattern of oblique diverging grooves"). Finally, this pattern is predominated by fine growth lines forming an otherwise smooth, shiny surface (Figs.

7A: IV, D). Only a vestige of the oblique grooves may still be visible. This surface structure is maintained to the aperture.

This general scheme is not completely realized in all Costa Rican Helicinidae, certain sections may be absent, for example, the pattern of oblique diverging grooves continues for the rest of the postembryonic shell and the smooth surface is absent. Apart from differences in detail, the pattern of the major part of the postembryonic shell does not change again and starts at the latest at the beginning of the second whorl (Fig. 7A, III–IV). Therefore, a section of this whorl is preferably described for species comparisons.

Embryonic Shell: If available, at least three specimens of each species or subspecies respectively were investigated for embryonic shell structures. Individuals were chosen randomly and depending on the preservation. Especially in cloud forest areas, the embryonic shell seems to erode very quickly.

Unless otherwise stated, relative descriptions refer to the structures of *Helicina funcki*.

Operculum: The operculum of most species of the Helicinidae is concentric and consists of two plates, an inner horny plate (attached to the foot) and an outer calcareous plate. The horny plate projects beyond the margins of the calcareous plate. In all Costa Rican species except for *Pyrgodomus*, the calcareous plate is thin and becomes thickened only towards the columellar edge, determining the shape of this margin, whereas the palatal margin is shaped by the further extending horny layer; the calcareous layer becomes indistinguishable and normally does not reach this margin.

Animal: Expecting species-specific differences in the mantle color of certain species, as many specimens as possible were documented as to their color, but due to considerable variation, especially among different populations, the comparison did not reveal many species-specific differences. A generalized description will be given for each species.

Radula: The helicinid radula consists of three groups of teeth: the centrals, the laterals and the marginals (Fig. 8). The central field is composed of an unpaired central or rhachidian tooth (R), which is flanked by three paired teeth, called A-, B-, and C-cen-



FIG. 8. Part of radula ribbon (shown in *Helicina funcki*); "A"–"C": respective central teeth, ap: accessory plate, cl: comb-lateral, R: rhachidian tooth; scale bar 100 μ m.

tral with the A-central aside to the rhachidian tooth (some authors such as Keen, 1960; Thompson, 1980, but not 1982; Stanisci, 1997, include the three paired teeth into the laterals). The laterals, also called the capituliform complex, are formed by two partially fused teeth, the inner comb-lateral (cl) and the accessory plate (ap). Within the Helicinidae, the comb-lateral is developed in two main types: (1) the true "comb"-lateral: a broad tooth with numerous cusps at the cutting edge (Fig. 8) or (2) a very strong tooth T- or mushroom shaped (also called T-lateral) without cusps (Fig. 246B). The marginals encompass numerous long, slender teeth in oblique rows that bear a varying number of acuminate cusps. The terminology follows Baker (1922a).

The radulae of the Costa Rican species of *Helicina* do not show many differences among the individual species, but within populations of the species themselves, there is some variation, especially regarding the number of cusps on the central teeth. A certain number of cusps is usually not exceeded, but the cusps are often vestigial or absent, forming a crenulate margin at the cutting edge. Throughout each radula, the different teeth are very uniformly developed with a very constant numbers of cusps.

The rhachidian tooth is triangular to trap-ezoid shaped and lacks cusps. The A- and B-centrals project laterally, with broad faces forming an oblique cutting edge. The C-central narrows towards its face and represents the outer tip of the central cutting edge.

The two teeth of the capituliform complex were always observed to be fused, and, under the conditions and the magnifications studied with the SEM, the demarcation line between the teeth was not visible. The cusps on the comb-lateral only show intraspecific fluctuations of one or two, but aberrant developments do occasionally occur (e.g., many more cusps or lacking any at all). The relative size of the cusps appears to be constant. In most species, the cusps slightly decrease in length towards both ends of the edge, with the inner a little longer. The accessory plate is usually slightly smaller than the comb-lateral and projects laterally.

With the occasional exception of the innermost tooth, the marginals increase in number of cusps outwards starting with 2–3 to more than 10. Two tendencies were recognized: (1) slowly and (2) rapidly increasing number of cusps; in the first, there are remarkably more teeth with 2, 3 and 4 cusps, that is, also more teeth with pronounced terminal cusps, whereas in teeth with more cusps the latter tend to arrange themselves laterally along the tip which is therefore turned sideways to bring the cutting edge into action.

In the account on the radula for the species, only the distinguishing features are outlined in addition to the figures.

Unless otherwise stated, the radulae of at least three specimens of each species and in some cases also of different populations were investigated. For *Helicina funcki* and *H. beatrix riopejensis* n. subsp. eight specimens were studied to check for intraspecific variability.

Female Reproductive System: Parts of the reproductive system of the Helicinidae show several peculiarities for which authors have introduced special terminology (Bourne, 1911; Baker, 1925 & 1926). Because terms were exchanged and confused, a summary is given, and the present use is indicated (Table 2, Fig. 9). The terminology implies certain functional aspects, but the function has been controversially discussed for different taxa (e.g., Bourne, 1911) and still remains partially doubtful, especially with respect to the structures for sperm storage. The terms used in this study follow the traditional usage and strike a balance between possible confusions, but will not be modified for functional correctness to avoid any fur-

TABLE 2. Terminology of the female reproductive system in Helicinidae.

Anatomical position	BOURNE (1911)	BAKER (1925)	BAKER (1926)	THOMPSON (1980)	Present study
	Parts of oviduct				
Direct continuation of slender primary oviduct	descending limb	first limb	right limb	ascending limb	ascending limb
Limb of V-organ leading into pedicel	ascending limb	-	left limb	pedicel**	descending limb
Basal portion of V-organ from invaginated constriction up to reception chamber	-	-	pedicel	pedicel**	pedicel
Portion of oviduct receiving several accessory organs	-	fertilization chamber	reception chamber	seminal receptacle**	reception chamber
Distal part of oviduct, parallel to rectum	ootype	secondary gonoduct or uterus	uterus	pallial oviduct	pallial oviduct
Accessory structures					
On top of V-organ	-	accessory sperm sac	-	accessory sperm sac	accessory sperm sac
On descending limb just above pedicel	receptaculum seminis	-	accessory sperm sac	accessory sperm sac	receptaculum seminis
Sac entering directly into reception chamber	-	-	secondary accessory sperm sac (for <i>Schastichella</i>)	-	no specific term
Ventral, associated with reception chamber	caecum of ootype	spermatheca or bursa copulatrix	ventral bursa	bursa copulatrix/ copulatory bursa	bursa copulatrix
Dorsal, associated with reception chamber or provaginal duct	provaginal sac*	provaginal sac	provaginal sac	provaginal sac	provaginal sac

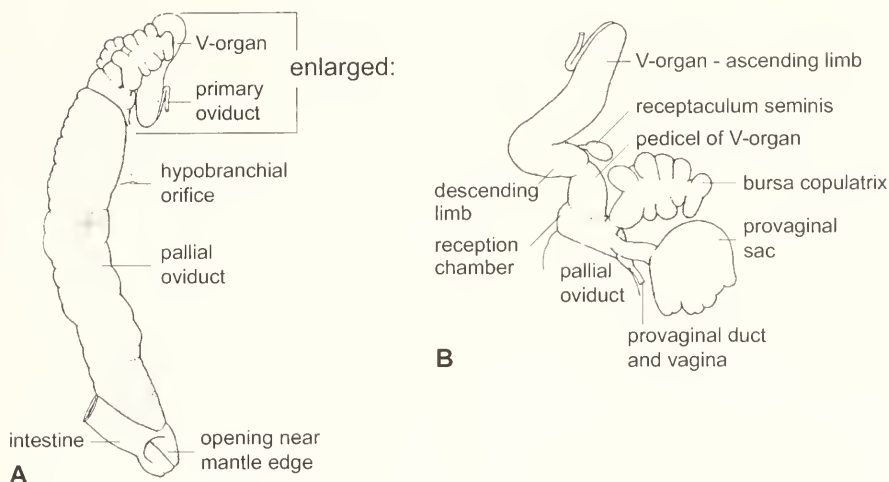


FIG. 9. Female reproductive system in Helicinidae (*Helicina orbiculata*), ovary to slender portion of the oviduct omitted, ventral view. A. Organs in natural position. B. Apical complex enlarged and artificially arranged to show the different organs and their connections (modified after Baker, 1926).

ther confusion until these aspects have been finally clarified. Furthermore, the term "pallial" only refers to the topographical position and not to ontogenetic origin.

The reproductive system of female Helicinidae consists of a folliculous ovary that discharges into a thin-walled spherical structure, which continues as the slender primary oviduct. This oviduct is curved anteriorly before it enters the V-organ. The V-organ is subdivided in an ascending limb, a descending limb, and a pedicel and leads into the reception chamber. The oviduct continues as an elongated pallial part parallel to the intestine and opens near the mantle edge. The descending limb of the V-organ

may receive the duct of a receptaculum seminis, or is associated with sac-like structures (accessory sperm sac) at its very beginning (e.g., *Lucidella*). Besides the oviduct (pedicel), the reception chamber is connected with a ventral bursa, a dorsal provaginal sac, and a provaginal duct that opens into the mantle cavity. Because of the two openings, the female system is called diallic.

Because the general structure is similar in Costa Rican *Helicina*, it is described as follows, and only specific deviations are added under each species.

The ascending limb of the V-organ is straight and a little longer than descending limb and

(Continued from opposite page)

* The caecum of the ootype and the provaginal sac *sensu* Bourne (1911) were differently interpreted by Baker. In 1925, he assigned the organs correctly as given in my Table, whereas in 1926, he exchanged this assignment of the terms, regarding his former interpretation as wrong. He pointed out that in Bourne's figure (1911: pl. XXXV, fig. 25) the caecum would clearly be located dorsally (as only is the provaginal sac) with respect to the oviduct. Actually, he disregarded the accurate description of the position of the organs. He was probably misled by the fact that in *Alcadia palliata* (C. B. Adams, 1849) the general appearance of this apical complex with both ventral bursa and provaginal sac elongated and without lobes differs somewhat from the mainland species that he had dissected.

*** Thompson misinterpreted the pedicel (term introduced by Baker, 1926) as the whole descending limb of the V-organ. In Helicinidae, it is demarcated by an invaginated constriction and subsequent distal swelling before entering into the reception chamber, also histologically differentiated. In the Ceresidae and Proserpinidae, which Thompson studied, the descending limb and a pedicel are not externally demarcated, but since histological data are lacking, the identification of the "descending" limb with the pedicel only (and absence of the "non-pedicel" part) is not verified for the two families.

*** Thompson intended to comply with other prosobranch terminology, but because both Latin and English terms were used (e.g., bursa copulatrix and copulatory bursa) for the same organ, "seminal receptacle" would be synonymous with "receptaculum seminis", a term being already in use for an accessory structure. Furthermore, as far as it is known just the reception chamber is not a place for sperm storage, i.e. a receptaculum seminis.

pedicel together, and in natural position it approximately reaches the transition of the reception chamber to the pallial oviduct. Situated between the limbs of the V-organ, a comparatively small, always simple sac-shaped receptaculum seminis enters the descending limb with a slender duct. The ventral bursa copulatrix is always lobed, but to a different extent. The provaginal sac is well developed, but rather simple shaped, and possesses a fairly long stalk as connection to the reception chamber. Contrary to the general scheme given above and the descriptions of other Central American species of *Helicina* by Baker (1926), the provaginal duct or vagina does not exist and the system is monaulic. The thick walls of the pallial oviduct are always variously folded, which is reflected in surface constrictions. A short, distinct portion just before the distal opening is dark brownish, whereas the remaining part of the reproductive system is whitish-opaque if not otherwise stated.

If material was sufficient the reproductive system of at least three females of each species or population were dissected. In addition, serial sections were studied for *Helicina funcki*, *H. tenuis*, *H. beatrix confusa*, *H. beatrix riopejensis* n. subsp., *H. gemma*, *Alcadia hojarasca*, and *Lucidella lirata* to confirm the results of the dissections.

In the drawings, the reproductive system is normally shown from the ventral side and the accessory organs of the apical part were artificially separated to allow an adequate presentation of this complex structure (Fig. 9B). If not otherwise stated, relative descriptions refer to the structures of *Helicina funcki*.

Morphometry and Sexual Dimorphism: Due to the paucity of material, the number of specimens of each population/species studied could not be standardized, but, as far as possible, maximized; the number of specimens is indicated in each case. The following measurements were analyzed: height, minor diameter, height of last whorl and columellar axis, extension of outer lip, volume and weight, if available. The major diameter is given only for comparison, but it is not included in diagrams, because the shells increase regularly in size, and it is therefore correlated with the minor diameter, which can be measured more exactly.

For the comparison with populations of unknown sex (e.g., INBio material, type material) the sex-independent mean value is always indicated in the diagrams by shading, it is given as the average of the mean values of both sexes. In this way, it more closely approaches the theoretical 1:1 distribution of females and males than the mean value of the total population.

When relations of the shell size of the different populations of one species to other parameters will be analyzed, the minor diameter is preferred over the shell height, because it is better correlated to the volume (shown for *Helicina funcki*, Fig. 30). The latter would display the size best, but the volume is normally not available for all populations.

Habitat: The description of the habitat is nearly exclusively based on the author's own field observations.

Distribution: In addition to the description, for the distribution within Costa Rica a detailed map is provided based on all records critically revised and the material studied. The sources of the localities will be indicated divided into recent collections (IR, INBio), and literature records and the other material examined.

Discussion: Here, mainly the taxonomical problems of each species will be discussed. For broader aspects, see the general Discussion.

REVISION OF THE COSTA RICAN HELICINIDAE

The following species are recognized for Costa Rica:

- Helicina (Tristramia) funcki* L. Pfeiffer, 1849
- Helicina (Tristramia) pitaisensis* Wagner, 1910
- Helicina (Tristramia) tenuis* L. Pfeiffer, 1849
- Helicina (Tristramia) echandiensis* n. sp.**
- Helicina (Tristramia) punctisulcata cuericiensis* n. subsp.**
- Helicina* ("Gemma") *beatrix beatrix* Angas, 1879
- Helicina* ("Gemma") *beatrix confusa* (Wagner, 1908)
- Helicina* ("Gemma") *beatrix riopejensis* n. subsp.**

Helicina ("Gemma") *talamancensis* (Richling, 2001)

Helicina ("Gemma") *gemma* Preston, 1903

***Helicina* ("Gemma") *monteverdensis* n. sp.**

***Helicina* ("Gemma") *escondida* n. sp.**

Helicina ("Gemma") *chiquitica* (Richling, 2001)

Pyrgodomus microdinus (Morelet, 1851)

Alcadia (*Microalcadia*) *hojarasca* (Richling, 2001)

Alcadia (*Microalcadia*) *boeckeleri* (Richling, 2001)

Lucidella (*Perenna*) *lirata* (L. Pfeiffer, 1847)

Questionable:

Helicina (*Oligyra*) *flavida* Menke, 1828

Helicina (*Tristramia*) *funcki*

L. Pfeiffer, 1849

Helicina funcki L. Pfeiffer, 1849: 121 (not figured)

Helicina funcki – L. Pfeiffer, 1850: 33, pl. 9, figs. 1, 2

Helicina funcki – L. Pfeiffer, 1852a: 361

Helicina tuncki [sic] – L. Pfeiffer, 1852b: 261–262

Helicina funckii [sic] – Sowerby, 1866: 288, pl. 273, fig. 271

Helicina funcki – Bland, 1866: 9

Helicina funcki – Reeve, 1874: pl. 17, fig. 152

Helicina funki [sic] – Angas, 1879: 484, pl. XL, fig. 7 (living animal): Costa Rica: Talamanca, all the coast region, and to the lower hills (Gabb)

Helicina funcki – von Martens, 1890: 33: Costa Rica: Talamanca, all the coast region, and to the lower hills (Gabb); Cache [Cachi? 09°50'N, 83°48'W, Cartago Province] (Rogers)

Helicina funcki var. a, b – Biolley, 1897: 4–5: Costa Rica: San Miguel, Sarapiquí, 200 m [about 10°19'N, 84°11'30"W, Alajuela Province], Tuis, 600 m [about 09°51'N, 83°35'W, Cartago Province]

Helicina funcki var. c, d – Biolley, 1897: 4–5: Costa Rica: Azahar de Cartago, 1,500 m, Tarbaca, 1,600 m [09°49'25"N, 84°06'39"W, San José Province]

Helicina funcki – Ancey, 1897: 87: E-Nicaragua: Greytown, N-Panama: Monkey Hill, near Colon (leg. Aillaud)

Helicina funcki – von Martens, 1900: 603-604: E-Nicaragua: Greytown; NE-Costa Rica: San Miguel, valley of the Sarapiquí, 200 m [about 10°19'N, 84°11'30"W, Alajuela Province]; Puerto Viejo [about 10°28'N, 84°00'30"W, Heredia Province] (Biolley), on

the borders of the Río San Juan [along borderline to Nicaragua in Alajuela, Heredia, Limón provinces, cannot be specified] (Pittier), E-Costa Rica: Tuis, 600 m [about 09°51'N, 83°35'W, Cartago Province] (Biolley, Pittier); Turrialba, 750 m [about 09°54'30"N, 83°41'W, Cartago Province] (Biolley), central Costa Rica: Azahar de Cartago [not clear, if referring to the town Cartago, ?about 09°52'N, 83°55'W, Cartago Province] and Tarbaca, 1,500-1,600 m [09°49'25"N, 84°06'39"W, San José Province], only the smaller varieties (Biolley); N-Panama: Monkey Hill, near Colon [in part]

Helicina (*Retorquata*) *funcki* – Wagner, 1905: 232-233

Helicina (*Retorquata*) *funcki costaricensis* Wagner, 1905: 233, pl. XIII, fig. 12 a–c: Costa Rica ("von San José [14 km NW of Upala, about 10°58'N, 85°08'W, Alajuela Province] in Costarica besitze ich Exemplare dieser Form, welche größer und einfarbig weiß sind, ferner ¼ bis ½ Umgang mehr aufweisen")

Helicina fucki [sic] – Wagner, 1910a: 306307, pl. 61, figs. 11–15: Neu Granada (obviously only in part of Panama), Costa Rica: Azachar Centajo, Tarbaca

Helicina funcki costaricensis – Wagner, 1910a: 307, pl. 61, fig. 16: Costa Rica: St. José [see above] and Sta. Clara [7.5 km NW of Upala, about 10°56'N, 85°05'W, Alajuela Province]; "eine ähnliche Form, jedoch mit deutlicher Kante am letzten Umgang und höherem Gewinde liegt in meiner Sammlung mit der Fundartsangabe Ylalag in Mexico"

Helicina funcki – Pilsbry, 1910: 503: Panama: Canal Zone: Tabernillo (Brown)

Helicina funcki – Pilsbry, 1920a: 3: Costa Rica: Guapiles, 980 ft. [about 10°14'N, 83°47'W, Limón Province] (Calvert)

Helicina deppeana parvidens Pilsbry, 1920a: 3 (not figured): Costa Rica: Juan Viñas, farther waterfall, 3300 ft., also on the road to Río Reventazon, 3000 ft. [about 09°54'N, 83°44'30"W, Cartago Province] (Calvert)

Helicina (*Tristramia*) *funcki funcki* – Baker, 1922a: 51

Helicina (*Tristramia*) *funcki parvidens* – Baker, 1922a: 51

Helicina (*Tristramia*) *funcki costaricensis* – Baker, 1922a: 51

Helicina funcki – Pilsbry, 1926a: 59, 69, 71, fig. 3C: Panama: Escobal on Gatun Lake (Chapin), Bocas del Toro Province: Mono Creek (Olsson), Gatun (Harrower), Canal

Zone: Barro Colorado Island and near Darien (Zetek)

Helicina funcki – Pilsbry, 1926b: 127: Costa Rica: Talamanca Valley, < 100 ft. [approximately 09°34'N, 83°W, not specified, Limón Province] (Olsson)

Helicina (Tristramia) funcki – Baker, 1926: 42: Panama: Gatun, Canal Zone (Harrower), pl. V fig. 8, pl. VI, fig. 9 (female and male reproductive system)

Helicina funcki – Pérez, 1994: 746: Costa Rica: La Selva [about 10°26'N, 84°W, Heredia Province]

Helicina funki [sic] – Monge-Nájera, 1997: 113: Costa Rica

Helicina funcki – Robinson, 1999: 434: USA: sometimes mistakenly imported

Synonymy

Helicina funcki costaricensis Wagner, 1905

Helicina deppeana parvidens Pilsbry, 1920

Original Description

“*Hel. testa conico-subglobosa, tenuiuscula, sub lente tenuissime oblique striatula, vix nitidula, flavida, roseo-nebulosa; spira conoidea, obtusiuscula; anfractibus 5,5 planiusculis, ultimo utrinque convexiore, obsolete angulato; apertura obliqua, semiovali; columella subarcuata, linea impressa verticali notata, basi subnodosa, in callum sensim tenuiorem retrorsum abiente; peristomate late expanso, margine supero subrepando. Diam. 13,5, altit. 9 mill.*”

From San Yago, New Granada (Funck).”

Type Material

BMNH 20010497.1–4: Santiago, New Granada, Funk, H. Cuming collection

The type lot contains four similar specimens. The shell that is slightly larger than the other three is **herein selected as lectotype** of *Helicina funcki* (Fig. 10). It shows the traces of some lead pencil painting which could have been applied to the specimen as a drawing aid, probably reflected in the dark shading visible in the figure in L. Pfeiffer (1850: pl. 9, figs. 1, 2). Furthermore, it is the only specimen that attains 13.5 mm in its greatest extension (not perpendicular to the shell axis). The height given in the original description cannot be attributed to a conventional adjustment of the shell. The specimen is yellowish, and the reddish tinge is barely visible, whereas it is well developed in the three paralectotypes in the second half of the body whorl between suture and the periphery.

Dimensions:

Lectotype BMNH 20010497.1:

10.6/11.9/13.2/10.7/7.9/8.8/8.2 mm

Paralectotypes BMNH 20010497.2–4:

10.1/11.5/12.6/10.2/7.3/8.3/7.7 mm

10.0/11.0/12.4/10.0/7.1/8.2/7.6 mm

10.0/11.1/12.4/10.1/7.4/8.2/7.9 mm

Type Locality

“San Yago, New Granada”, this most probably refers to Santiago, which today belongs to Panama, Veraguas Province.

Type Material of Synonymous Taxa or Similar Species

Helicina funcki costaricensis Wagner, 1905

Type Material: MIZ 8989: Costa Rica, Sta. Clara, 250 m alt., Biolley legit

In the original description Wagner gives Costa Rica as the origin of the new subspecies and mentions additional specimens from San



FIG. 10. *Helicina funcki*, lectotype, BMNH 20010497.1, height 10.6 mm; scale bar 5 mm.

José, which are said to be of greater size and of uniformly white color, the description being obviously based on further unspecified material. In his collection stored in the MIZ, there are two lots: the typical one with the locality mentioned later (Wagner, 1910a), as given above and the one from San José. The syntypes MIZ 8989 consist of two specimens, a yellowish-greenish one and a reddish tinged one. In comparing the figures in Wagner (1905, 1910a), it is obvious that different specimens were illustrated: the later figure shows a yellowish-greenish specimen somewhat more elevated and with a more strongly developed denticle at the transition of the outer lip into the columella. Thus, the reddish specimen was first to be depicted and has therefore been **selected here as lectotype** (Fig. 11). It displays a slight crack in the last whorl which, however, did not result in any deformation or damage in the shell. The specimen was dead collected, whereas the paralectotype was collected alive, complete with its operculum.

Dimensions:

Lectotype MIZ 8989a:

12.0/13.2/14.6/11.8/8.7/9.7/9.3 mm

Paralectotype MIZ 8989b:

12.3/13.1/14.6/11.9/8.9/10.1/9.5 mm

Type Locality: "Costa Rica"; restricted by type selection to Sta. Clara, 250 m a.s.l. [7.5 km NW of Upala, about 10°56'N, 85°05'W, Alajuela Province]

"Santa Clara" is a name used for various localities in Costa Rica. Biolley mentions it several times as a collecting site, also "Delicias near Santa Clara" and a "San José" (see "Discussion" for *Helicina funcki*

costaricensis) that is definitively not the capital. This combination suggests the identification with the village of Santa Clara near Upala, because Las Delicias and San José are nearby. The exact altitude of Santa Clara is 40 m, but it is known that in former times (personal communication with Zaidett Barrientos) the whole region was called "Llanuras de Santa Clara" [plains of ...]. Therefore, in case it was not just an inaccurate measurement of the altitude, it is likely that the specimens were collected a little to the southeast of the village approaching the Cordillera de Guanacaste.

Helicina deppeana parvidens Pilsbry, 1920

Type Material: Holotype ANSP 105286 (Fig. 12), Paratype ANSP 105252 (original designation)

Type Locality: Costa Rica: "Juan Viñas, farther waterfall, 3300 ft." [about 09°54'N, 83°44'30"W, Cartago Province]

Examined Material

LEG. I. RICHLING

Guanacaste: *N Santa Elena: Reserva Sta. Elena, Sendero Río Negro, about 10°20'31"N, 84°47'53"W, 1,550 m a.s.l.*: 14.08.1999: (IR 924); *Sendero at Mirador Gerardo, 10°22'19"N, 84°48'25"W, 1,450 m a.s.l.*: 14.08.1999: (IR 928); 19.02.2000: (IR 1230)

N of Nuevo Arenal: area of primary rain forest, 10°33'32"N, 84°51'40"W, 800 m a.s.l.: 05.03.1999: (IR 737); "Las Pavas" (private reserve in preparation), secondary rain for-



FIGS. 11–12. *Helicina* spp. FIG. 11. *Helicina funcki costaricensis*, lectotype, MIZ 8989a, height 12.0 mm; scale bar 5 mm. FIG. 12. *Helicina deppeana parvidens*, holotype, ANSP 105286, height 10.0 mm; scale bar 5 mm (photograph: D. Robinson).

- est, about 10°33'30"N, 84°51'53"W, 800 m a.s.l., to 10°33'26"N, 84°51'57"W, 760 m a.s.l.: 05.03.1999: (IR 742); 17.08.1999: (IR 952); 24.02.2000: (IR 1273); (IR 1331); 03.2001: (IR 1637)*
NW Nuevo Arenal, "Eco Lodge", Sendero Cabana, about 10°34'37"N, 84°55'35"W, 750 m a.s.l., 18.08.1999: (IR 955)
Parque Nacional Rincón de Vieja: trail from Aguas calientes to Las Pailas, about 10°46'00"N, 85°19'13"W, 800 m a.s.l.: 20.08.1999: (IR 972); E Casona Sta. Maria, trail to Canal, 10°45'57"N, 85°17'06"W, 750 m a.s.l.: 21.08.1999: (IR 979)
Alajuela: Near Volcán Arenal, trail along volcano in rainforest, about 10°29'07"N, 84°42'55"W, 720 m a.s.l.: 24.02.1998: (IR 390); 01.08.1999: (IR 884); on Heliconiaceae, 25.02.2000: (IR 1286)
Heredia: S Puerto Viejo de Sarapiquí, Zona Protectora La Selva, near OTS-Station, about 10°25'53"N, 84°00'18"W, 60 m a.s.l., 05.09.1999: (IR 1061); 06.09.1999: (IR 1062); 13.02.2000: (IR 1182); (IR 1184)
Limón: Parque Nacional Cahuita, trail from Cahuita to Puerto Vargas, coastal forest with coco palms and swampy areas: 09°44'01"N, 82°49'48"W, 1–5 m a.s.l.: 11.03.1997: (IR 107); (IR 106); (IR 108); about 09°43'27"N, 82°50'28"W, 4 m a.s.l.: 10.03.1999: (IR 757); 07.08.1999: (IR 897); 08.08.1999: (IR 898); 04.03.2000: (IR 1312); 14.03.2001: (IR 1555), (IR 1630), (IR 1639); 15.03.2001: (IR 1557), (IR 1648); 09°43'13"N, 82°50'39"W, 4 m a.s.l.: 13.09.1999: (IR 1095); near Puerto Vargas, 09°42'49"N, 82°49'20"W, 1 m a.s.l.: 08.08.1999: (IR 907)
Refugio Nacional de Fauna Silvestre Gandoca-Manzanillo, S Manzanillo, trail along coast line to S, coastal forest, about 09°38'06"N, 82°38'26"W, 50 m a.s.l., 14.9.1999: (IR 1096); 5.3.2000: (IR 1320); (IR 1322); (IR 1642)
Near Cruce Penshurt, mouth delta of Río Estrella, Aviarios del Caribe, about 09°48'30"N, 82°54'W, 20 m a.s.l., 09.08.1999: (IR 912)
About 9 km W of Matina, road Limón to Siquirres, a little stream up Río Barbilla, small banana plantation, about 10°03'29"N, 83°22'24"W, 70 m a.s.l., 12.03.2001: (IR 1545)
S Siquirres, road Limón to Siquirres, along footpath stream up Río Pacuarito, 10°05'38"N, 83°28'11"W, 110 m a.s.l., 18.03.2001: (IR 1612); (IR 1613)
Siquirres, along footpath stream up Río Siquirres and along a southern tributary, 10°05'37"N, 83°30'32"W, 100 m a.s.l., 11.03.2001: (IR 1623); 19.03.2001: (IR 1617)
W Guayacán, abandoned banana plantation, 10°01'53"N, 83°32'14"W, 520 m a.s.l., 03.09.1999: (IR 1079); (IR 1080); 12.09.1999: (IR 1090); 17.03.2001: (IR 1608)
W Liverpool, Mexico: near Río Blanco, 09°56'37"N, 83°09'41"W, 35 m a.s.l.: 13.03.1997: (IR 150); near Río Blanco, abandoned area with bananas and some old trees, 09°58'32"N, 83°08'32"W, 35 m a.s.l.: 14.02.1998: (IR 274); 21.02.1999: (IR 627); footpath along small creek and through bush, 09°59'04"N, 83°08'04"W, 40 m a.s.l.: 16.02.2000: (IR 1191); 22.02.2001: (IR 1406); (IR 1408)
S Liverpool: near Río René, swampy area and forest, 09°57'33"N, 83°08'15"W, 20 m a.s.l.: 13.03.1997: (IR 148); (IR 140); along Río Victoria, 09°56'01"N, 83°10'24"W, 80 m a.s.l.: 05.03.1998: (IR 465)
SW Liverpool: Río Quito, at bridge, 09°57'11"N, 83°10'37"W, 40 m a.s.l.: 04.03.1998: (IR 448); E of Río Peje, forest on little hill, 09°57'46"N, 83°13'26"W, 270 m a.s.l.: 12.03.1997: (IR 131); Río Peje and small tributary, 09°56'35"N, 83°14'01"W, 110 m a.s.l.: 12.03.1997: (IR 126); (IR 127); Río Peje, bordering forest, 09°56'23"N, 83°14'06"W, 160 m a.s.l.: 09.03.1999: (IR 753); along Río Peje, bordering forest with palms, 09°55'46"N, 83°13'15"W, 135 m a.s.l.: 04.03.1998: (IR 441); 09.03.1999: (IR 751); 03.03.2000: (IR 1300); (IR 1302); 13.03.2001: (IR 1552)
N Shiroles: along Quebrada Kirio, 09°35'38"N, 82°57'20"W, 100 m a.s.l.: 12.03.1999: (IR 763); 09.08.1999: (IR 911); 16.03.2001: (IR 1596); (IR 1644); Cerro Mirador, along trail, 09°36'37"N, 82°57'43"W, 430 m a.s.l.: 16.03.2001: (IR 1599)
W Bribri, road to Uatsi, about 09°38'11"N, 82°51'48"W, 30 m a.s.l.: abandoned field with Heliconiaceae and Eucalyptus: 12.03.1999: (IR 766); 15.09.1999: (IR 1114); wooded valley within banana plantation, 50 m a.s.l.: 15.3.2001: (IR 1572); at crossing with Río Carbón, 30 m a.s.l.: 17.3.1997: (IR 183);
W Uatsi, along Río Uatsi, 09°37'30"N, 82°53'30"W, 60 m a.s.l., 15.03.2001: (IR 1632)
Zona Protectora Tortuguero, near Tortuguero, about 10°34'N, 83°31'W, 10 m a.s.l.: Sendero Ranita: 10.3.2000: (IR 1348); N of village: 16.03.2001: (IR 1620); 21.03.2001: (IR 1653)

Cartago: W Turrialba, near *Catie*, forest along road Turrialba to Siquirres, 09°53'01"N, 83°39'17"W, 610 m a.s.l., 15.03.2000: (IR 1350)

Puntarenas: Near Monteverde, about 10°17'24"N, 84°48'04"W: small piece of forest along road to reserve, 1,330 m a.s.l.: 27.02.1997: (IR 22); 1 km before entrance on road to reserve, 1,500 m a.s.l.: 26.07.1999: (IR 826); 1999: (IR 1391); 13.8.1999: (IR 927); *Bosque de los Niños*, 10°17'59"N, 84°48'44"W, 1,380 m a.s.l.: 29.07.1999: (IR 860)

Zona Protectora Arenal-Monteverde: Reserva Biológica Bosque Nuboso Monteverde (about 10°18'08"N, 84°47'41"W, 1,500–1,650 m a.s.l.): 27.07.1999: (IR 843); 18.02.2000: (IR 1194); (IR 1199); (IR 1627); Sendero Bosque Nuboso: 25.02.1997: (IR 14); 24.02.1999: (IR 628); Sendero Roble: 18.02.1998: (IR 301); Sendero Chomogo: 25.02.2001: (IR 1435)

Monteverde, Cerro Plano, Finca Ecológica, Sendero Mirador, 10°18'47"N, 84°49'30"W, 1,330 m a.s.l., 25.02.1999: (IR 651); 28.07.1999: (IR 859); 15.08.1999: (IR 946); 20.02.2000: (IR 1246)

About 4 km N Santa Elena, Skywalk, 10°18'33"N, 84°49'42"W, 1,330 m a.s.l., 20.02.1998: (IR 332)

INBIO COLLECTION

Guanacaste: Zona Protectora Arenal-Monteverde: Santa Elena, sendero Encantado, 10°21'57"N, 84°47'27"W, 1,200 m a.s.l., leg. Kattia Martínez, 21.06.1996: 8 ads. (INBIO 1498638)

Zona Protectora Tenorio: Río San Lorenzo, Tierras Morenas, 10°36'38"N, 84°59'42"W, 1,050 m a.s.l., leg. Gladys Rodríguez, 28.10.1995: 1 ad. (INBIO 1485411); Tenorio, Alrededores de la estación, 10°36'51"N, 85°00'07"W, 900 m a.s.l., leg. Gladys Rodríguez, 18.09.1996: 1 ad. (INBIO 1498593)

Parque Nacional Rincón de la Vieja: Sector Las Pailas: 4.5 km SW del Volcán Rincón de la Vieja, 10°46'36"N, 85°21'07"W, 800 m a.s.l., leg. malacological staff of INBIO, 09.12.1992: 1 ad. (INBIO 1466644); sendero Pailas, 10°46'36"N, 85°21'07"W, 800 m a.s.l., leg. Karla Taylor, 23.08.1995: 3 ads., 1 s.ad. (INBIO 1498739); Sector Santa María: 10°45'58"N, 85°18'19"W, 800 m a.s.l., leg. Dunia García, 14.10.1995: 1 ad. (INBIO 1487945); sendero Bosque Encantado, 10°46'36"N, 85°21'07"W, 800 m

a.s.l., leg. Karla Taylor, 23.08.1995: 1 ad. (INBIO 1498744)

Parque Nacional Guanacaste: Estación Góngora, 10°53'22"N, 85°28'33"W, 580 m a.s.l.: leg. Zaidett Barrientos, 11.02.1994: 2 ads. (INBIO 1480300); leg. Dunia García, 20.10.1994: 1 juv. (INBIO 1478682); 2 juvs. (INBIO 1478739); 2 ads. (INBIO 1483409); leg. Dunia García, 28.10.1994: 1 ad. (INBIO 1480475); leg. Dunia García, 08.03.1995: 1 ad. (INBIO 1488083); leg. Dunia García, 28.06.1995: 1 ad., 3 juvs. (INBIO 1484993); Sector Góngora [río Góngora], 10°53'22"N, 85°28'33"W, 580 m a.s.l.: leg. Kattia Martínez, 26.05.1995: 1 juv. (INBIO 1498514) Parque Nacional Guanacaste: Sector Orosi (antes: Maritza), sendero Casa Fram, 10°57'40"N, 85°29'45"W, 600 m a.s.l., leg. Zaidett Barrientos, 15.07.1996: 3 ads. (INBIO 1494681); Río Tempisque, 10°57'45"N, 85°29'05"W, 600 m a.s.l., leg. Dunia García, 08.03.1996: 1 juv. (INBIO 1488078)

Parque Nacional Guanacaste: La Cruz, 9 km S de Santa Cecilia, Estación Pitilla: 10°59'25"N, 85°25'38"W, 700 m a.s.l.: leg. Petrona Rios, 09.12.1994: 1 ad. (INBIO 1480289); Lado S del Río Orosi, leg. Calixto Moraga, 16.08.1994: 3 ads. (INBIO 1480319); leg. Calixto Moraga, 23.08.1994: 1 ad. (INBIO 1480318); 10°59'33"N, 85°25'46"W, 700 m a.s.l.: leg. malacological staff of INBIO, 08.01.1993: 1 ad. (INBIO 1463787); leg. Calixto Moraga, 10.07.1993: 1 juv. (INBIO 1467560); Sendero Nacho, 10°59'33"N, 85°25'46"W, 700 m a.s.l.: leg. malacological staff of INBIO, 13.10.1993: 1 ad. (INBIO 1463946); Sendero Mena, 400 m W de la Estación Pitilla, 10°59'25"N, 85°25'51"W, 700 m a.s.l.: leg. Calixto Moraga, 09.01.1994: 1 ad. (INBIO 1480043); Fila Orosillo, 10°59'02"N, 85°26'01"W, 900 m a.s.l.: leg. Calixto Moraga, 20.04.1994: 1 ad. (INBIO 1480329); Finca del Estado: Casa de Roberto, 11°00'09"N, 85°25'33"W, 600 m a.s.l.: leg. Calixto Moraga, 22.08.1994: 1 s.ad. (INBIO 1480342) La Esperanza, 6 km E de Santa Cecilia de la Cruz, 11°00'42"N, 85°22'45"W, 400 m a.s.l., leg. Calixto Moraga, 09.01.1994: 1 ad. (INBIO 1480050)

Alajuela: Reserva Biológica Los Angeles, 7 km NE de los Angeles Norte de San Ramón, 10°12'12"N, 84°29'10"W, 1,100 m a.s.l., leg. Zaidett Barrientos, 06.11.1995: 1 ad., 2 s.ads. (INBIO 1482570)

Reserva Biológica San Ramón, 10°13'30"N, 84°35'17"W, 800 m a.s.l.: leg. malacological

staff of INBio, 15.02.1994: 1 ad. (INBio 1477816); leg. Gerardo Carballo, 10.07.1994: 1 ad. (INBio 1476150); Sendero Liz, leg. Gerardo Carballo, 08.08.1994: 1 ad. (INBio 1476214)

Sector Colonia Palmareña, 10°14'09"N, 84°33'15"W, 700 m a.s.l., leg. Eida Fletes, 13.04.1995: 1 ad. (INBio 1485385)

Zona Protectora Arenal-Monte Verde: Sector Alemán, Finca dos Ases, 10°17'56"N, 84°46'08"W, 1,140 m a.s.l.: leg. Zaidett Barrientos, 13.10.1994: 1 ad. (INBio 1468276); leg. Kattia Martínez, 04.12.1995: 2 ads. (INBio 1485227); *Sendero Alemán*, 10°17'59"N, 84°45'38"W, 1,080 m a.s.l.: leg. Kattia Martínez, 18.08.1994: 1 ad. (INBio 1480101); 19.08.1994: 1 ad. (INBio 1478523); *Sector Peñas Blancas, Estación Alemán*, 10°18'09"N, 84°44'52"W, 900 m a.s.l.: leg. Kattia Martínez, 11.10.1994: 2 ads. (INBio 1498802); 11.12.1994: 1 ad. (INBio 1480605)

Parque Nacional Guanacaste-Rincón de la Vieja, *Estación San Cristóbal*, 10°52'55"N, 85°23'26"W, 600 m a.s.l.: leg. Dunia García, 08.01.1995: 5 ads., 2 s.ads. (INBio 1488065); leg. malacological staff of INBio, 18.08.1995: 8 ads., 5 s.ads. (INBio 1498494)

Sector las Cubas, Bosque Urbina, 10°53'41"N, 84°47'20"W, 40 m a.s.l., leg. Kattia Martínez, 25.04.1994: 1 ad. (INBio 1466940)

Caño Negro: Veracruz, 10°50'22"N, 84°52'52"W, 35 m a.s.l.: leg. Kattia Flores, 14.02.1997: 1 juv. (INBio 1487125); *Finca Delicias*, 10°54'01"N, 84°47'20"W, 35 m a.s.l.: leg. Kattia Flores, 14.12.1996: 1 ad. (INBio 1487043); 01.11.1997: 1 ad. (INBio 1487611); *en el Pueblo*, 10°53'38"N, 84°47'20"W, 35 m a.s.l.: leg. Kattia Flores, 09.10.1994: 1 ad. (INBio 1480029); 07.04.1995: 5 ads. (INBio 1501040)

Refugio Nacional de Vida Silvestre Caño Negro: Caño Negro, San Antonio, Finca Juan Cubano 2, 10°54'50"N, 84°45'12"W, 35 m a.s.l., leg. Kattia Flores, 16.11.1996: 1 ad. (INBio 1487878)

Monte Cele, sendero La Tepezcuintle, 10°57'27"N, 85°24'20"W, 700 m a.s.l., leg. Dunia García, 09.09.1995: 4 ads. (INBio 1488042)

Estación Playuelas, 50 m del Río Frío, 10°57'29"N, 84°44'55"W, 40 m a.s.l., leg. Kattia Martínez, 08.01.1994: 4 ads. (INBio 1479506)

Sector Playuelas, 10°57'29"N, 84°45'15"W, 35 m a.s.l.: leg. Kattia Martínez, 21.08.1996:

2 ads. (INBio 1498571); leg. Kattia Flores, 08.11.1996: 1 ad. (INBio 1487809)

Heredia: *Frente al bosque de la hoja*, 10°04'13"N, 84°05'40"W, 1,800 m a.s.l., leg. Zaidett Barrientos, 14.05.2000: 1 ad. (INBio 3562231)

Limón: *Reserva Indígena Talamanca: Sector Amubri*, 09°30'53"N, 82°57'19"W, 70 m a.s.l.: 14.06.1994: 1 ad. (INBio 1477585); 15.06.1994: 1 ad. (INBio 1477569); 26.09.1994: 1 ad. (INBio 1483302); 4 s.ads. (INBio 1483303); 1 juv. (INBio 1483376); 1 ad. (INBio 1483382); 1 s.ad. (INBio 1483388); 2 ads. (INBio 1483392); 1 ad. (INBio 1483407); 2 s.ads. (INBio 1483408); 27.09.1994: 1 ad. (INBio 1483381); 1 ad. (INBio 1483389); 2 s.ads. (INBio 1483402); 29.09.1994: 2 s.ads. (INBio 1483403); 1 ad. (INBio 1483394); 30.09.1994: 2 s.ads. (INBio 1483395); 2 s.ads. (INBio 1483401); 18.10.1994: 1 ad. (INBio 1483390); 1 ad. (INBio 1483386); 19.10.1994: 1 s.ad. (INBio 1483383); 1 ad. (INBio 1483387); 1 s.ad. (INBio 1483396); 27.11.1994: 1 ad. (INBio 1483398); 28.11.1994: 1 s.ad. (INBio 1483378); 1 s.ad. (INBio 1483385); 29.11.1994: 1 s.ad. (INBio 1483397); 30.11.1994: 1 ad. (INBio 1483400) (all leg. Gerardina Gallardo); *Amubri, Sendero Soki*, 09°30'53"N, 82°57'19"W, 70 m a.s.l.: leg. Angela Mora Maroto, 17.04.1995: 1 ad. (INBio 1484735); leg. Gerardina Gallardo, 17.05.1994: 4 ads. (INBio 1467294); 4 ads. (INBio 3395382); leg. Angela Mora Maroto, 22.04.1995: 3 ads. (INBio 1485382); leg. Angela Mora Maroto, 04.08.1995: 1 ad. (INBio 1485365); leg. Gerardina Gallardo, 27.11.1996: 3 ads., 1 s.ad. (INBio 1493444) *Reserva Indígena Talamanca: Cerca Río Lari*, 09°32'57"N, 82°58'25"W, 80 m a.s.l.: leg. Gerardo Carballo, 17.06.1994: 1 ad. (INBio 1476073); *Suirí, orillas del Río Telire*, 09°33'56"N, 82°55'50"W, 30 m a.s.l.: leg. Gerardina Gallardo, 25.11.1996: 1 ad., 2 s.ads. (INBio 1487336) *Reserva Biológica Hitoy Cerere: Sector Miramar*, 09°38'03"N, 83°00'45"W, 300 m a.s.l.: leg. Zaidett Barrientos, 08.10.1994: 1 ad. (INBio 1475720); 1 ad. (INBio 1475725); *Senderos a Río Moin*, 09°37'44"N, 83°00'32"W, 150 m a.s.l.: leg. Zaidett Barrientos, 08.11.1994: 2 juvs. (INBio 1475228); 1 ad. (INBio 1475234); *Hitoy Cerere*, 09°37'50"N, 83°00'52"W, 300 m a.s.l.: leg. Gerardo Carballo, 12.05.1994: 3 ads., 1 s.ad. (INBio 1476376); leg. Gerardo Carballo, 13.06.1994: 4 ads. (INBio

1476490); leg. Gerardo Carballo, 04.07.1994: 2 ads. (INBio 1475694); leg. Marianella Segura, 07.12.1994: 1 ad. (INBio 1480272); *Sendero Moín*, 09°37'50"N, 83°00'52"W, 300 m a.s.l.: 14.01.1994: 3 ads. (INBio 1475930); 27.02.1994: 1 ad. (INBio 1476687); 1 ad. (INBio 1476688) (all leg. Gerardo Carballo)

Reserva Biológica Hitoy Cerere: Cruce entre Sendero Revienta Pechos y Sendero Espavel, 09°39'12"N, 83°00'58"W, 600 m a.s.l.: leg. Alexander Alvarado Mendez, 24.04.1999: 1 ad. (INBio 1497851); *Sector Hitoy Cerere, Sendero Catarata*, 09°40'18"N, 83°01'45"W, 100 m a.s.l.: leg. Gerardo Carballo, 22.02.1994: 1 ad. (INBio 1476262); *Sendero Tepezcuitle*, 09°40'22"N, 83°01'40"W, 140 m a.s.l.: 25.04.1999: 2 ads. (INBio 1497862); 2 ads. (INBio 3090624); 05.07.1999: 1 ad. (all leg. Alexander Alvarado Mendez) (INBio 1497905); *Sendero Bobócara*, 09°40'31"N, 83°00'31"W, 200 m a.s.l.: leg. malacological staff of INBio, 10.01.1993: 1 ad. (INBio 1466444); *Sendero Toma de Agua*, 09°40'31"N, 83°01'36"W, 100 m a.s.l.: 20.04.1994, leg. Zaidett Barrientos: 2 ads. (INBio 1473832); leg. Gerardo Carballo: 1 ad. (INBio 1476246); leg. Zaidett Barrientos, 08.09.1994: 1 ad. (INBio 1475438); *Estación Hitoy Cerere*, 09°40'35"N, 83°01'36"W, 100 m a.s.l.: leg. malacological staff of INBio, 15.11.1993: 3 ads. (INBio 1463392); 400 m NE de la Estación de Hitoy Cerere, *Sendero la "Finca"*, 09°40'35"N, 83°01'26"W, 110 m a.s.l.: 03.06.2000: 1 ad. (INBio 3098418); 20.07.1999: 1 s.ad. (INBio 1497844); 27.09.2000: 2 ads. (INBio 3091789) (all leg. Alexander Alvarado Mendez); *Sendero Chato*: 09°40'41"N, 83°01'26"W, 100 m a.s.l., leg. Marianella Segura, 14.07.1994: 1 s.ad. (INBio 1478197)

Refugio Nacional de Vida Silvestre Gandoca-Manzanillo: Sector Gandoca, Camino a Gandoca, 09°38'04"N, 82°38'37"W, 10 m a.s.l.: 28.04.1999: 5 juvs. (INBio 3097941); *Sector Manzanillo*: 1 km S de la escuela, 09°37'31"N, 82°39'36"W, 4 m a.s.l., 02.02.2000: 2 ads. (INBio 3097906); *Camino a Gandoca*, 09°38'13"N, 82°38'40"W, 100 m a.s.l., 28.01.2000: 2 ads. (INBio 3097895); *Sendero a Gandoca*, 09°38'04"N, 82°38'43"W, 8 m a.s.l., 04.02.2000: 2 s.ads. (INBio 3097899) (all leg. Alexander Alvarado Mendez)
1 km S de Punta Cocles, 09°38'17"N, 82°43'25"W, 40 m a.s.l., leg. Zaidett

Barrientos, 20.08.1996: 1 ad., 1 juv. (INBio 1487850)

Parque Nacional Cahuita: Sector Cahuita: 800 m E de la Casetilla, 09°44'00"N, 82°49'57"W, 10 m a.s.l., 05.11.1999: 1 s.ad., 1 juv. (INBio 3096430); *Sector Puerto Vargas: Sendero a Cahuita*, 09°43'43"N, 82°49'11"W, 0 m a.s.l., 01.09.1999: 3 ads. (INBio 3095846); 600 m E de la Casetilla, 09°42'54"N, 82°48'58"W, 8 m a.s.l., 27.09.2000: 1 juv. (INBio 3091796) (all leg. Alexander Alvarado Mendez)

Isla Uvita, frente al muelle de Limón, 09°59'45"N, 83°00'50"W, 5 m a.s.l., leg. Alexander Alvarado Mendez, 11.10.2000: 2 ads., 1 juv. (INBio 3315386)

Zona Protectora Río Pacuare: 1.3 km NW de la Estación Barbilla, 09°59'25"N, 83°28'04"W, 500 m a.s.l., leg. Alexander Alvarado Mendez, 02.11.2000: 1 ad. (INBio 3315302)

Reserva Indígena Barbilla-Dantas: Sector Colonia Puriscaleña, 10°00'17"N, 83°23'02"W, 300 m a.s.l., leg. Alexander Alvarado Mendez, 03.03.2000: 2 juvs. (INBio 3098016)

Sector Guápiles: 10°11'51"N, 83°51'22"W, 300 m a.s.l., leg. Alexander Alvarado Mendez, 08.03.2000: 2 ads., 1 s.ad. (INBio 3097950)

Orillas del río Aguas Frías, 10°24'05"N, 83°35'60"W, 10 m a.s.l.: leg. Elías Rojas, 29.11.1996: 3 ads. (INBio 1487980)

Finca Montaña Grande, 10°31'39"N, 83°43'33"W, 10 m a.s.l.: 400 m N de la estación, a orillas de la quebrada: 13.09.1993: 3 ads. (INBio 1498610); 300 m N de la estación: 21.09.1996: 1 ad. (INBio 1501097); 600 m N de la estación Cedrales: 13.11.1996: 2 juvs. (INBio 1501055); 14.12.1996: 1 juv. (INBio 1498623) (all leg. Elías Rojas)

Finca Toty Castro, 1.7 km S de la estación Cedrales, 10°31'39"N, 83°43'33"W, 10 m a.s.l., leg. Elías Rojas, 16.10.1996: 1 ad. (INBio 1501098)

Refugio Nacional de Vida Silvestre Barra del Colorado: Pococí, Colorado, Sector Cerro Cocorí, 30 km N de Cariari, 10°35'39"N, 83°42'59"W, 160 m a.s.l.: leg. malacological staff of INBio, 10.12.1993: 6 ads. (INBio 1465446); leg. malacological staff of INBio, 04.10.1994: 3 ads. (INBio 1478061); leg. Elías Rojas, 10.05.1994: 5 ads. (INBio 1483360); leg. Elías Rojas, 24.08.1994: 1 ad., 1 s.ad. (INBio 1480255); leg. Elías Rojas, 10.09.1994: 1 ad. (INBio 1483208); 1

- juv. (INBio 1483209); leg. Elias Rojas, 13.09.1994: 2 ads. (INBio 1480261); 1 juv. (INBio 1480281); leg. Elias Rojas, 10.10.1994: 1 ad. (INBio 1483017); leg. Elias Rojas, 05.12.1994: 1 ad. (INBio 1467174)
- Refugio Nacional de Vida Silvestre Barra del Colorado: Barra del Colorado, Estación Sardinias: 10°38'52"N, 83°43'52"W, 50 m a.s.l.: 05.01.1994: 1 ad. (INBio 1478283); 10.02.1994: 4 ads. (INBio 1484010); 12.05.1994: 1 ad., 1 s.ad. (INBio 1484585); 5 ads., 1 s.ads. (INBio 1484587); 6 ads. (INBio 1484589); 24.05.1994: 1 s.ad. (INBio 1478305); 11.07.1994: 4 s.ads., 2 juv. (INBio 1484432); 25.07.1994: 1 ad. (INBio 1478294); 28.08.1994: 1 ad. (INBio 1480051); 12.10.1994: 3 juv. (INBio 1484372); 3 ads., 1 s.ad., 2 juv. (INBio 1484372); 12.10.1994: 3 ads., 1 s.ad., 2 juv. (INBio 1484374); 16.10.1994: 3 ads. (INBio 1484013); 22.10.1994: 2 ads. (INBio 1484991); 7 ads., 1 s.ad. (INBio 1485284); 5 ads., 1 s.ad., 2 juvs. (INBio 1485285); 7 ads., 1 s.ad., 2 juvs. (INBio 1485289); 2 juvs. (INBio 1485290); 09.11.1994: 2 s.ads. (INBio 1480044); 09.12.1994: 1 ad. (INBio 1480041); 01.02.1995: 1 ad., 1 s.ad. (INBio 1485145); 02.06.1995: 1 ad. (INBio 1484748); 4 ads. (INBio 1484749) (all leg. Flor Araya); 10°39'11"N, 83°44'21"W, 15 m a.s.l.: leg. malacological staff of INBio: 13.01.1994: 1 ad. (INBio 1478017); 16.04.1994: 1 ad. (INBio 1477915); 800 m N de la Estación Sardinias, Sendero Tono, 10°39'05"N, 83°44'31"W, 50 m a.s.l.: leg. malacological staff of INBio, 21.11.1993: 1 juv. (INBio 1465699); 1 ad. (INBio 1465700)*
- Cartago: Parque Nacional Tapantí-Macizo de La Muerte: Sendero Oropéndola, 09°45'09"N, 83°47'08"W, 1,260 m a.s.l.: leg. Rosa Guzman, 03.10.1997: 1 ad. (INBio 1488194); Estación Quebrada Segundo, 09°45'45"N, 83°47'18"W, 1,360 m a.s.l.: leg. Roberto Delgado, 18.10.1994: 1 ad. (INBio 1479646); leg. Roberto Delgado, 03.07.1995: 1 ad. (INBio 1487842)*
- Monumento Nacional Guayabo: Turrialba, Santa Teresita, 09°58'26"N, 83°41'42"W, 1,000 m a.s.l., leg. Zaidett Barrientos, 16.12.1994: 1 ad. (INBio 1476052)*
- Puntarenas: Quebrada Chanchera, 800 m W de la Playa, 08°37'26"N, 83°26'39"W, 1 m a.s.l., leg. Socorro Avila, 08.12.1996: 1 ad. (INBio 1486976)*
- San Luis, Finca Buen Amigo, 10°16'36"N, 84°47'48"W, 1,100 m a.s.l., leg. Zobeida Fuentes, 26.06.1995: 1 ad. (INBio 1484382)*
- Zona Protectora Arenal-Monte Verde: Reserva Biológica Bosque Nuboso Monte Verde: Sendero Brillante, 10°17'59"N, 84°47'10"W, 1,520 m a.s.l.: leg. Kattia Martinez, 17.06.1994: 2 ads. (INBio 1466835); Sendero Bosque Nuboso, 10°17'59"N, 84°47'36"W, 1,600 m a.s.l.: 24.05.1994: 5 ads. (INBio 1466884); 3 ads. (INBio 1466954); 2 ads. (INBio 1467003); 25.05.1994: 1 ad. (INBio 1466842); 1 ad. (INBio 1466870); 2 ads. (INBio 1466891); 1 ad. (INBio 1466905); 1 ad. (INBio 1467024); 14.06.1994: 3 ads., 2 sads. (INBio 1467031); 15.07.1994: 2 ads. (INBio 1479528); 16.07.1994: 2 ads. (INBio 1479539); 25.09.1995: 1 ad. (INBio 1498806); 28.10.1995: 1 ad. (INBio 1498590); 20.10.1996: 4 ads. (INBio 1498828) (all leg. Kattia Martinez); Sendero Bosque Nuboso, 10°17'59"N, 84°47'36"W, 1,520 m a.s.l.: leg. Zaidett Barrientos, 14.10.1994: 1 s.ad., 1 juv. (INBio 1468141); 1 ad. (INBio 1468211); 1 ad. (INBio 1468212); Sendero el Camino, 10°18'03"N, 84°47'15"W, 1,560 m a.s.l.: 23.05.1994: 5 ads., 1 s.ad. (INBio 1466912); 1 s.ad. (INBio 1466947); 23.05.1994: 1 s.ad. (INBio 1466996); 2 ads. (INBio 1467010); 25.05.1994: 1 ad. (INBio 1466863); 1 s.ad. (INBio 1466968); 10.06.1994: 7 ads. (INBio 1480426); 14.07.1994: 2 ads., 1 s.ad. (INBio 1480126); 2 ads. (INBio 1480128); 5 ads. (INBio 1480129); 1 ad. (INBio 1480149); 08.08.1994: 3 ads. (INBio 1479517); 2 ads. (INBio 1479550); 1 juv. (INBio 1479838); 16.09.1994: 1 ad. (INBio 1480098); 10.10.1994: 1 ad. (INBio 1485422); 26.09.1995: 1 ad. (INBio 1498807) (all leg. Kattia Martinez); Sendero el Roble, 10°18'16"N, 84°47'27"W, 1,600 m a.s.l.: leg. Kattia Martinez, 08.11.1994: 1 ad. (INBio 1480132); Sendero Chomogo, 10°18'22"N, 84°47'23"W, 1,640 m a.s.l.: 13.08.1994: 1 ad. (INBio 1480152); 10.10.1994: 1 ad. (INBio 1485426); 08.12.1994: 1 ad. (INBio 1477521); 15.12.1994: 1 ad. (INBio 1484687); 06.03.1995: 1 ad. (INBio 1485441) (all leg. Kattia Martinez); Sendero Bosque Eterno, 10°18'22"N, 84°47'40"W, 1,600 m a.s.l.: 09.06.1994: 1 ad. (INBio 1480119); 06.08.1994: 1 s.ad. (INBio 1466793); 28.10.1995: 1 ad. (INBio 1498581) (all leg. Kattia Martinez); Sendero el Río, 10°18'29"N, 84°47'37"W, 1,600 m a.s.l.: 15.07.1994: 1 juv. (INBio 1479353); 08.12.1994: 3 ads. (INBio 1480127); 1 ad. (INBio 1480130); 1 ad. (INBio 1480131);*

04.07.1995: 1 s.ad. (INBio 1485234); 1 ad. (INBio 1485235) (all leg. Kattia Martinez); *Estación la Casona*, 10°18'11"N, 84°47'50"W, 1,520 m a.s.l.: 08.09.1994: 1 ad. (INBio 1479451); 22.09.1995: 3 ads. (INBio 1498804); 28.10.1998: 3 ads. (INBio 1498632) (all leg. Kattia Martinez); 10°18'15"N, 84°47'46"W, 1,520 m a.s.l., leg. malacological staff of INBio, 28.07.1994: 5 ads. (INBio 1477749) *Finca tomas*, por Casa Boby, 10°18'12"N, 84°48'22"W, 1,520 m a.s.l., leg. Kattia Martinez, 24.10.1995: 1 s.ad. (INBio 1498808) *Cerro Plano*, 10°18'58"N, 84°49'09"W, 1,300 m a.s.l., leg. Kattia Martinez, 02.09.1996: 1 ad. (INBio 1498652)

OTHER SOURCES

COSTA RICA

Guanacaste: Tilaran [about 10°28'30"N, 84°58'30"W], leg. Univ. Alabama, M. Smith coll.: 6 ads. (UF 95283)

1.7 mi S Tilaran on road to Quebrado Grande [about 10°27'N, 84°58'W], leg. R.W. McDiarmid, 28.08.1971: 2 ads., 1 s.ad. (UF 214166)

10 mi W Tilaran [about 10°26'N, 85°06'W], leg. Ronald Heyer, 06.08.1964: 1 ad. (UF 214163)

Monte Verde [about 10°18'N, 84°47'W], leg. Savage & Scott, 13–16.05.1964: 6 ads., 3 s.ads. (UF 214170)

Alajuela: San Carlos [about 10°20'N, 84°26'W], leg. McGinty coll., ex Preston & Tomlin: 3 ads. (UF 160150)

Cariblanca [about 10°17'N, 84°12'W], Sarapiquí, 600 m a.s.l., P. Biolley (#267): 5 ads. (MHNN)

Chemin de Sarapiquí, S. Miguel [about 10°19'N, 84°11'30"W], leg. P. Biolley: 11 ads. (MHNN)

Tesalia [Tetsalia?, about 10°21'N, 84°24'W], leg. R. W. McDiarmid, 18–20.07.1971: 1 ad. (UF 214164)

Heredia: Puerto Viejo [de Sarapiquí, about 10°28'N, 84°00'30"W], leg. P. Biolley: 2 ads. (ZMB 103242)

Río Frio, Standard Fruit Co., 10°20'N, 83°53'W, 300 ft., leg. Michael J. Corn, 21.11.1969: 1 ad. (UF 214160); 22.11.1969: 2 s.ads. (UF 214172)

[not: "Alajuela"], Río Frio [about 10°20'N, 83°53'W], leg. Michael J. Corn, 05.05.1970: 1 ad. (UF 214161); 15.05.1970: 1 ad. (UF 214171)

Limón: Los Diamantas Farm, 11.08.1971: 1 ad. (UF 69846); Los Diamantes Farm, 12 mi SE Guapiles [about 10°11'N, 83°37'W], leg. R.W. McDiarmid, 13.08.1971: 1 ad. (UF 214167)

Moin, hill #1 [about 10°N, 83°04'W], leg. C. Little, 29.09.1967: 1 ad. (UF 214158)

Cueva Castil, near Limon [about 10°N, 83°02'W], leg. Colin Little, 30.08.1967: 5 ads. (UF 214165)

Puerto Limon, football field adjacent to Standard Fruit Box Factory [about 10°N, 83°02'W], leg. D.G. Robinson (TU-954), 19.05.1984: 1 ad. (UF 155820)

Along road cut, along south side of Río Banano, opposite La Bomba, 09°54'49.7"N, 83°03'56.4"W, leg. D.G. Robinson & J.M. Montoya, 21.09.1998 (APHIS PPQ USDA) Pandora [about 09°43'N, 82°58'W], leg. Jay Savage, 01.05.1964: 1 ad. (UF 214156); leg. F. G. Thompson (FGT-100), 05.08.1964: 3 ads. (UF 214157)

3.2 km N Pandora [about 09°45'N, 82°58'W], leg. F.G. Thompson (FGT-98), 04.08.1964: 8 ads, 1 s.ad. (UF 214155)

1 km NW of Cahuita, 09°44.5'N, 82°50.9'W", leg. F.G. Thompson (FGT-5616), 25.02.1996: 1ad. (UF 258427)

Trib[utary] to Río Moin [Valle de Talamanca], 572 500 E, 397 600 S, 430 m a.s.l. [09°37'45"N, 83°00'18"W], leg. E.L. Raiser (ELR-082), 10.08.1994: 1 ad. and in alcohol (UF 41438) (UF 41437); leg. F. Alvando (ELR-087), 11.08.1994: 2 ads. (UF 41442)

Amubre [about 09°32'N, 82°57'30"W], leg. Norman Scott, 16.03.1964: 1 ad. (UF 214168)

San José: Tarbaca [about 09°49'25"N, 84°06'39"W], leg. P. Biolley: 2 ads. (ZMB 103246)

2 lots mixed: Cartago: 1. Azahar de Cartago [not clear, if referring to the town Cartago, ?about 09°52'N, 83°55'W], San José: 2. Tarbaca [about 09°49'25"N, 84°06'39"W], leg. P. Biolley: 10 ads. (MHNN)

Cartago: 2 lots mixed: Cartago: 1. Azahar de Cartago [not clear, if referring to the town Cartago, ?about 09°52'N, 83°55'W], San José: 2. Tarbaca [about 09°49'25"N, 84°06'39"W], leg. P. Biolley: 10 ads. (MHNN) Tapanti, 4300 ft. [about 09°47'N, 83°48'W], leg. F. G. Thompson (FGT-23), 26.06.1963: 1 ad. (UF 214169)

Turrialba [about 09°54'30"N, 83°41'W], ex coll. S.G.A. Jaeckel: 2 ads. (HNC 39842);

coll. Bosch, ex Rolle, ex Wagner: 6 ads. (SMF 180790/6); Turrialba, versant de l'Atlantique, 750 m [about 09°54'30"N, 83°41'W], leg. P. Biolley (#146), 07.1893: 4 ads. (MHNN)

Valleé de Tuis [about 09°51'N, 83°35'W], H. Pittier, 9.1893 ex coll. Wiegmann: 1 ad. (ZMB 70633)

Cartago?: Cache [Cachí?, about 09°50'N, 83°48'W], leg. Roger, ex Godwin & Salvin: 1 ad. (ZMB 40836)

Puntarenas: 1.5 mi NE Monte Verde [about 10°19'N, 84°47'W], leg. R.W. McDiarmid (RWM-11), 17.02.1966: 6 ads. (UF 214162)

Costa Rica, without locality further specified: leg. Beal-Maltbie coll., ex W. F. Webb coll.: 4 spec. (UF 237539); leg. H. G. Lee, ex G.D. Robinson, W.F. Webb: 1 ad. (UF 166943); leg. Univ. Alabama, T.H. Aldrich coll. (THA-8213), ex Webb: 1 ad. (UF 95254); 1 ad. (UF 214110); leg. P. Biolley: 4 ads. (MHNN); leg. Carmiol: 2 ads. (ZMB 103244); ex Fulton: 3 ads. (ZMB 64488); 1 ad. (ZMB 103245)

NICARAGUA

Not further specified: Sumichrast: 2 ads. (UF 214108)

PANAMA

Bocas Del Toro: Colon Island, leg. McGinty coll.: 2 ads. (UF 185608); Isla Colon, ca. 12 km NNW of Bocas del Toro, 09°25'00"N, 82°16'23"W, leg. F.G. Thompson (FGT-4726), 19.09.1990: 1 ad. (UF 167537); Isla Colon, limestone knoll along E coast, 5 km NNE of Bocas del Toro, 09°23'05"N, 82°14'09"W, leg. F.G. Thompson (FGT-4727), 20.09.1990: 1 ad. (UF 167538)

N end of Isla San Cristobal, 09°17'28"N, 82°15'51"W, leg. F.G. Thompson (FGT-4730), 21.09.1990: 1 ad. (UF 167541)

Isla Bastimentos, 0.5 km NE of Bastimentos Town on trail to Wizard Beach, 09°20'59"N, 82°12'15"W, 60 m a.s.l., leg. F.G. Thompson (FGT-4731), 22.09.1990: 1 ad. (UF 167544)

Ojo de Agua, Filo Almirante, 09°17'32"N, 82°27'43"W, 300 m a.s.l., leg. F.G. Thompson (FGT-4733), 24.09.1990: 6 ads. (UF 167551)

Colón, Canal Zone: 0.5 mi SE Achioté, S. R. Telford, 12.1969, 1 ad. (UF 214173); 4.8 km SE Achioté, leg. F.G. Thompson (FGT-1130), 27.04.1969: 20 ads. (UF 214154)

0.8 km SW Madden Dam, leg. F.G. Thompson (FGT-1131), 02.05.1969: 1 ad. (UF 214159)

N bank Chagres River, 6 km NNE Gamboa, leg. S.R. Telford, 22.04.1969: 1 ad. (UF 214174)

Canal Zone, not further specified: leg. Univ. Alabama, M. Smith coll., ex Clark 5 ads., 1 s.ad. (UF 95284); leg. Univ. Alabama, M. Smith coll.: 11 ads. (UF 95285)

Panama, without locality further specified: leg. Beal-Maltbie coll., ex W. Webb coll. (UF 237401)

Description

Shell (Fig. 335A–C): Conical-subglobose, solid, relatively large sized and dull to slightly shiny. Color: basic color yellowish to whitish-opaque, towards apex and on upper half of whorls often a more or less intensive tinge ranging from reddish-brown to flesh colored, in some specimens involving the whole shell with exception of outer lip. The color is slightly overlapped with fine light to transparent patches and lines giving the shell a special ornamentation. Surface textured with fine growth lines and oblique grooves of different individual orientations but of same general direction (Fig. 14), causing the dull appearance. Embryonic shell of about 1 whorl; 4–4⁵/₈ (lectotype: 4¹/₂) subsequent whorls nearly straight and only very slightly convex; last whorl with a touch of angulation on the periphery; whorls equally extending in size, forming a very regular, blunt spire. Suture very slightly impressed. Aperture oblique and nearly straight, last whorl only very slightly descending, inserting exactly at periphery or just below it. Outer lip independent of color of whorls, always yellowish-whitish, remarkably thickened and broadly expanded, upper palatal region slightly sinuate. Reflection nearly rectangular to the whorl; transition to columella with a more or less pronounced denticle. Columella slightly curved, its tran-

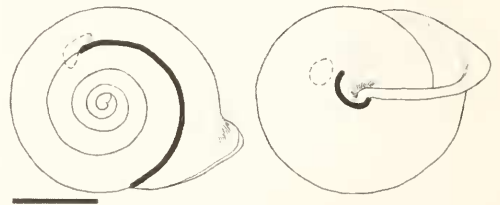


FIG. 13. Axial cleft and muscle attachments of *Helicina funcki*, IR 757; scale bar 5 mm.

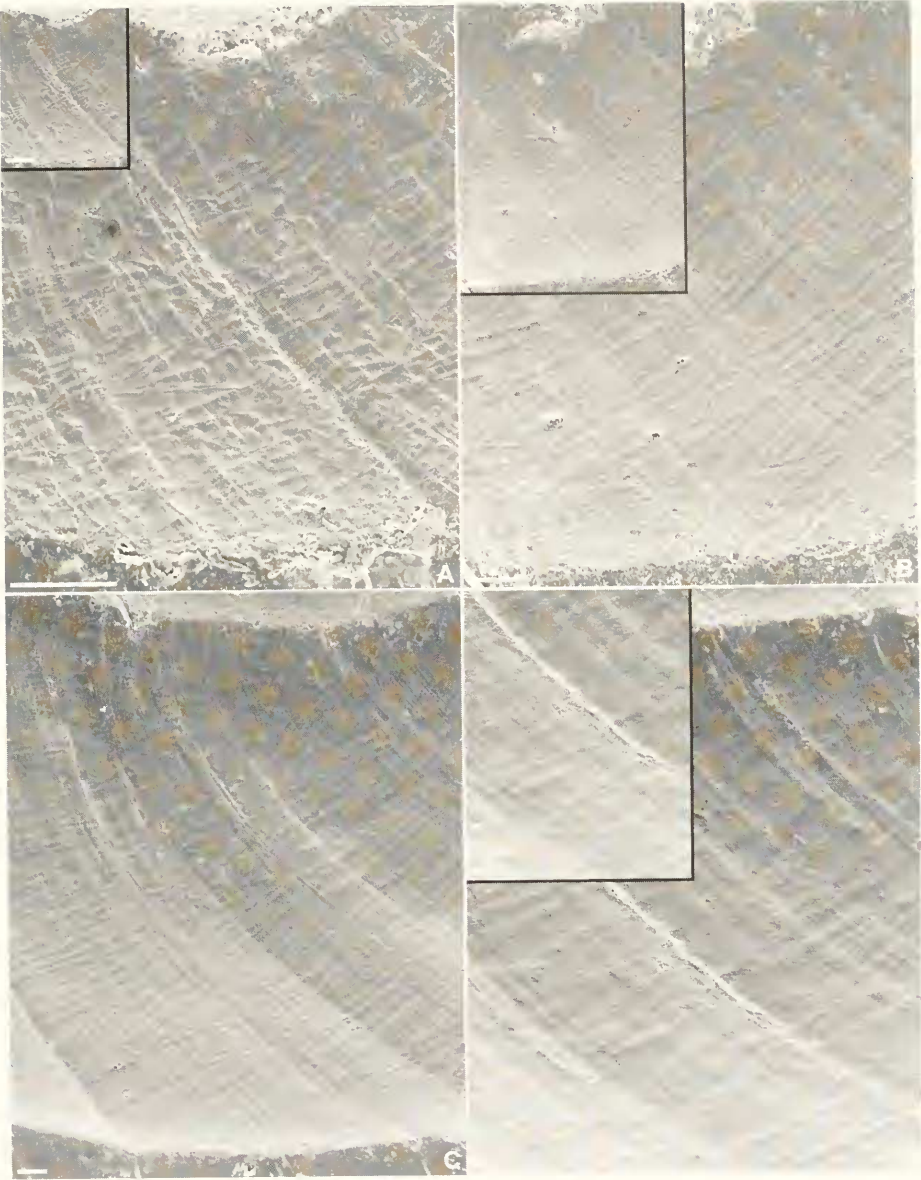


FIG. 14. Teleoconch surface structure of *Helicina funcki*. A. On 1st whorl. B. On 2nd whorl. C. On 3rd whorl. D. On 4th whorl (inset same magnification as in C); scale bar 100 μ m.

sition to body whorl marked with a perpendicularly impressed line or even a groove. Basal callus weakly developed and nearly completely smooth or very slightly granulated.

Juvenile specimens exhibit a roundly carinated periphery sometimes bearing periostracal spiral lines.

Internal Shell Structures: (Fig. 13)

Teleoconch Surface Structure: In *Helicina funcki*, the transitional structure is followed by a pattern of oblique diverging grooves, which is maintained in all whorls (Fig. 14B–D). The grooves only increase in length and become more widely spaced.

Embryonic Shell: The surface is structured with pits arranged in concentric lines (Fig. 15A). The diameter of these pits is approximately equal to the interspacial distance between the pits in a line as well as between the lines of pits themselves, although the arrangement is somewhat irregular. This is

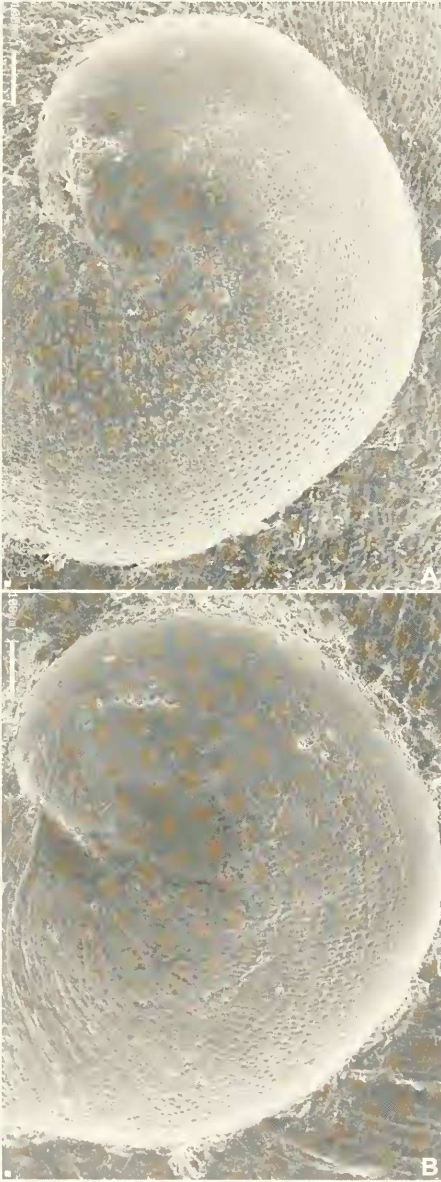


FIG. 15. Embryonic shell of *Helicina funcki*, A. Typical. B. Irregularities during growth; scale bar 100 μm .

the typical structure for *Helicina funcki*, but deviations also occur (Fig. 15B). The “compressed” pattern obviously results from irregularities experienced during growth (in the present case, during the younger part) which caused a different form of the embryonic shell and more closely spaced growth lines resulting in a reduction of the diameter (Fig. 15A: 1040 μm , Fig. 15B: 930 μm).

Concerning the size of the embryonic shell, the type material falls within the range of Costa Rican lowland populations (e.g., Cahuita), whereas specimens from higher altitudes of Monteverde consistently develop a much larger embryonic shell.

Diameter: 954 μm (± 41) (870–1,040) ($n = 16$) (IR 1630, IR 1639, IR 1642, IR 1648, Cahuita); 1,160 μm (± 43) (1,060–1,240) ($n = 20$) (IR 843, Monteverde); 980 μm (± 40) (940–1,040) ($n = 4$) (BMNH 20010497.1–4, type lot, lectotype: 1,000 μm); 970 μm (± 50) (9201,020) ($n = 2$) (MIZ 8989, type lot of *Helicina funcki costaricensis*, lectotype: 1020 μm).

Operculum (Fig. 16): Only slightly calcified, calcareous plate not fully extended over horny plate, leaving a free margin, thickened towards columellar side. Color dark reddish-brown to nearly black, only the margin transparent. Columellar side slightly S-shaped, upper end acute and pointed or nearly rectangular, lower end rounded, but slightly truncated towards the columella.

Animal (Fig. 337A, B): The color of the animal does not show any great variation, either at different sites or within the populations. Sole

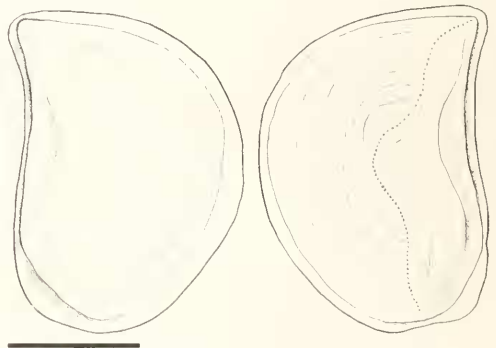


FIG. 16. Operculum of *Helicina funcki*, IR 757; scale bar 2.5 mm.

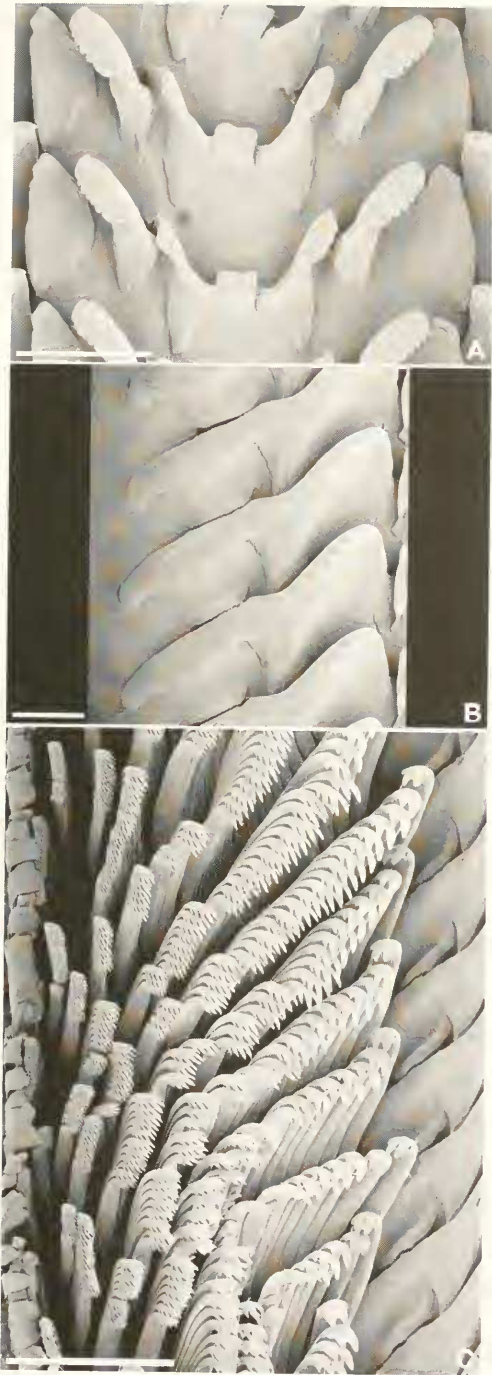


FIG. 17. Radula of *Helicina funcki*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 μ m (A, B), 100 μ m (C).

and sides of the foot are whitish-yellowish changing gradually to dark brown-greyish towards the upper side and head. The tentacles are also dark brown-greyish with a light tip. The mantle has a whitish-greenish pigmentation shining through the shell, thus providing the live specimens with a somewhat greenish appearance. The mantle only bears a dark color in juvenile specimens (Fig. 337B), being sometimes spotted with yellow, thus causing those juvenile individuals to appear darker.

Radula (Fig. 17): The cusps on the A- and C-central are vestigial, only the B-central with 4–5 more or less-well developed cusps. Comb-lateral with 7–9 cusps, cusps on marginals slowly increasing in number. Radula with about 70–105 rows of teeth.

Female Reproductive System (Figs. 18, 19): The receptaculum seminis enters at the middle of the inner side of the descending limb of the V-organ. It is a cylindrical, slender

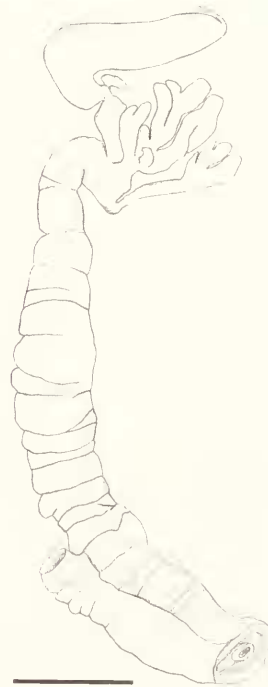


FIG. 18. Female reproductive system of *Helicina funcki*, IR 1312; scale bar 2 mm.



FIG. 19. Variability of the female reproductive system of *Helicina funcki*, IR 1312; scale bar 2.5 mm.

sac. The bursa copulatrix consists of numerous remarkably elongated lobes, some of which are always further subdivided. The provaginal sac is irregularly shaped, dorsoventrally flattened and bears lobe-structures at its distal side. The stalk is comparatively long and deeply curved anteriorly, as is the adjacent part of the reception chamber. The pallial oviduct is relatively long

and shows mainly transversal constrictions. In Figure 19, the right drawing shows the genital for a slightly immature specimen. The main difference consists in the much less thickened pallial oviduct, in which, except for a slight enlargement, the final shape of the accessory structure is already developed.

Morphometry and Sexual Dimorphism (Tables 3–4, Figs. 21–28)

From my own material, all adult specimens of known sex and populations with at least a few specimens of each sex were compared. A few populations with scanty material were included because of their otherwise undocumented origin.

The measurement of the weight is especially difficult in *Helicina funcki*, because a considerable part of the weight results from the strongly developed, broadly expanded outer lip. In Fig. 20, the increase of weight during growth is illustrated for the population from Cahuita (juveniles were studied from lot IR 1312). An additional non-mature shell from Rio Peje is included as an example for heavily-shelled specimens to demonstrate that the increase of weight during juvenile growth period continues at about the same rate. Shells

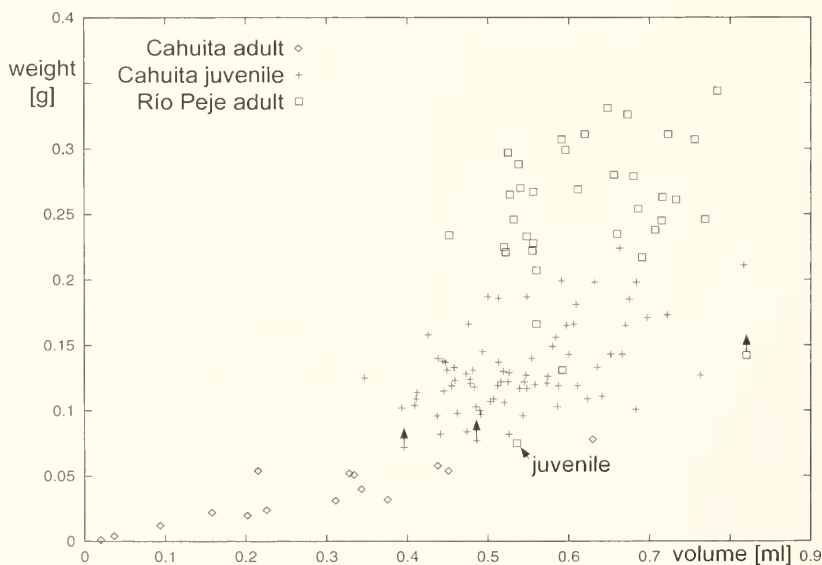


FIG. 20. Increase of weight during growth of *Helicina funcki* from Cahuita (juveniles IR 1312), compared also with adults from Rio Peje (one juvenile included); arrows indicate "thin-lipped" adults; juvenile = shells without expanded lip.

TABLE 3. Measurements of different populations of *Helicina funcki* from material collected by the author, given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

"Rincón de la Vieja" (altitude 800 m) lots IR 972, IR 979							"Mirador Gerardo" (altitude 1450 m) lots IR 924, IR 928, IR 1230				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	11.14	0.33	10.80	11.52	4	11.05	0.48	10.55	11.74	4
Height	m	10.60	0.32	10.22	11.04	4	10.17	0.11	10.04	10.34	4
Maj. diam.	f	12.02	0.31	11.57	12.63	4	12.42	0.36	11.96	12.96	4
Maj. diam.	m	11.56	0.69	10.66	12.36	4	11.90	0.12	11.67	12.07	4
Min. diam.	f	10.84	0.23	10.53	11.22	4	11.19	0.31	10.78	11.67	4
Min. diam.	m	10.39	0.56	9.58	11.05	4	10.48	0.08	10.36	10.65	4
Outer lip	f	7.95	0.20	7.56	8.11	4	8.17	0.14	7.92	8.36	4
Outer lip	m	7.83	0.52	7.13	8.76	4	7.83	0.26	7.49	8.25	4
Last whorl	f	9.08	0.17	8.78	9.30	4	9.15	0.27	8.82	9.48	4
Last whorl	m	8.86	0.27	8.43	9.30	4	8.61	0.06	8.49	8.68	4
Col. axis	f	8.73	0.17	8.50	8.97	4	8.62	0.32	8.08	9.10	4
Col. axis	m	8.14	0.13	7.96	8.29	4	7.89	0.11	7.67	8.09	4
Weight	f	0.078	0.008	0.066	0.094	4	0.137	0.025	0.117	0.187	4
Weight	m	0.093	0.032	0.032	0.132	4	0.142	0.015	0.125	0.162	4
Volume	f	0.471	0.031	0.435	0.515	4	0.491	0.031	0.452	0.553	4
Volume	m	0.409	0.053	0.342	0.471	4	0.400	0.005	0.390	0.408	4

"Monteverde - Finca Ecológica" (altitude 1330 m) lots IR 859, IR 946, IR 1246							"Monteverde" (altitude 1500 m) lots IR 843, IR 927, IR 1194, IR 1435, IR 1627				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	10.96	0.22	10.65	11.31	4	11.31	0.33	10.24	12.17	18
Height	m	10.03	0.22	9.70	10.32	3	10.29	0.38	9.71	11.55	15
Maj. diam.	f	11.91	0.43	11.33	12.54	4	12.73	0.36	11.70	13.38	18
Maj. diam.	m	11.09	0.44	10.43	11.70	3	12.10	0.34	11.54	12.98	15
Min. diam.	f	11.16	0.36	10.45	11.72	4	11.45	0.34	10.25	12.35	18
Min. diam.	m	9.94	0.33	9.45	10.34	3	10.77	0.37	10.19	11.55	15
Outer lip	f	8.04	0.21	7.75	8.30	4	8.16	0.20	7.40	8.65	18
Outer lip	m	7.65	0.30	7.34	8.09	3	7.85	0.23	7.15	8.54	15
Last whorl	f	9.02	0.25	8.56	9.30	4	9.39	0.25	8.57	10.09	18
Last whorl	m	8.32	0.30	7.88	8.55	3	8.71	0.32	8.26	9.74	15
Col. axis	f	8.55	0.19	8.16	8.86	4	8.82	0.27	8.14	9.45	18
Col. axis	m	7.88	0.27	7.58	8.28	3	7.98	0.26	7.62	8.81	15
Weight	f	0.156	0.037	0.105	0.198	4	0.174	0.018	0.137	0.235	18
Weight	m	0.126	0.046	0.057	0.177	3	0.132	0.024	0.075	0.188	15
Volume	f	0.444	0.028	0.407	0.490	4	0.521	0.039	0.385	0.653	18
Volume	m	0.345	0.020	0.315	0.365	3	0.420	0.035	0.368	0.518	15

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"Las Pavas" (altitude 800 m) lots IR 952, IR 955, IR 1273, IR 1637						"Tortuguero" (altitude 0–10 m) lots IR 1348, IR 1620, IR 1653					
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	12.12	0.22	11.81	12.75	7	12.22	1.13	11.09	13.34	2
Height	m	11.11	0.48	10.15	12.08	5	11.73	0.21	11.52	11.94	2
Maj. diam.	f	13.38	0.32	12.93	14.08	7	14.08	0.78	13.31	15.25	3
Maj. diam.	m	12.30	0.35	11.85	13.00	5	13.27	0.09	13.17	13.36	2
Min. diam.	f	12.11	0.18	11.61	12.44	7	12.66	0.77	11.84	13.82	3
Min. diam.	m	11.03	0.34	10.60	11.60	5	11.78	0.16	11.62	11.93	2
Outer lip	f	8.74	0.23	8.32	9.23	7	9.40	0.85	8.55	10.25	2
Outer lip	m	8.40	0.28	7.99	8.75	5	8.81	0.01	8.80	8.82	2
Last whorl	f	10.14	0.10	10.00	10.40	7	10.36	0.86	9.50	11.22	2
Last whorl	m	9.31	0.32	8.76	9.96	5	9.69	0.03	9.66	9.72	2
Col. axis	f	9.33	0.13	9.17	9.75	7	9.24	0.48	8.52	9.81	3
Col. axis	m	8.49	0.40	7.51	9.23	5	8.72	0.08	8.64	8.80	2
Weight	f	0.152	0.035	0.103	0.233	7	0.147	0.081	0.061	0.268	3
Weight	m	0.151	0.020	0.128	0.197	5	0.177	0.062	0.115	0.239	2
Volume	f	0.636	0.035	0.593	0.703	7	0.731	0.089	0.602	0.865	3
Volume	m	0.473	0.042	0.404	0.549	5	0.568	0.003	0.565	0.570	2

"La Selva" (altitude 60 m) lots IR 1061, IR 1062, IR 1182						"Guayacán" (altitude 520 m) lots IR 1079, IR 1090, IR 1608					
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	12.65	0.29	12.16	13.06	9	12.14	0.34	11.47	12.55	5
Height	m	11.62	0.36	10.92	12.26	9	11.50	0.31	11.19	11.80	2
Maj. diam.	f	14.06	0.21	13.56	14.37	9	13.18	0.36	12.69	13.62	5
Maj. diam.	m	13.37	0.23	12.78	13.82	9	12.70	0.17	12.45	12.89	3
Min. diam.	f	12.88	0.14	12.51	13.09	9	11.97	0.27	11.65	12.42	5
Min. diam.	m	12.00	0.18	11.51	12.32	9	11.41	0.10	11.27	11.56	3
Outer lip	f	9.56	0.24	9.03	10.18	9	8.73	0.11	8.48	8.88	5
Outer lip	m	9.08	0.29	8.30	9.47	9	8.52	0.04	8.48	8.55	2
Last whorl	f	10.58	0.19	10.21	10.95	9	10.14	0.29	9.66	10.43	5
Last whorl	m	9.86	0.27	8.98	10.22	9	9.61	0.07	9.54	9.68	2
Col. axis	f	9.77	0.17	9.38	10.00	9	9.34	0.24	8.88	9.56	5
Col. axis	m	8.93	0.21	8.37	9.35	9	8.76	0.11	8.63	8.92	3
Weight	f	0.236	0.036	0.134	0.277	9	0.191	0.032	0.138	0.233	5
Weight	m	0.219	0.044	0.141	0.278	9	0.175	0.004	0.171	0.179	2
Volume	f	0.729	0.037	0.652	0.783	9	0.615	0.040	0.533	0.669	5
Volume	m	0.580	0.041	0.505	0.638	9	0.534	0.001	0.533	0.534	2

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"México" (altitude 40 m) lots IR 274, IR1191, IR 1406							"Río Peje" (altitude 160 m) lots IR 751, IR 1300, IR 1552				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	11.22	0.23	10.92	11.68	4	12.54	0.33	11.56	13.64	17
Height	m	10.40	0.16	10.15	10.62	6	11.68	0.40	10.88	12.55	20
Maj. diam.	f	13.21	0.30	12.82	13.64	4	13.91	0.32	13.17	14.65	17
Maj. diam.	m	12.11	0.37	11.32	12.55	6	13.13	0.31	12.61	13.97	20
Min. diam.	f	11.98	0.29	11.59	12.40	4	12.74	0.29	11.93	13.27	17
Min. diam.	m	10.90	0.28	10.36	11.29	6	11.80	0.24	11.34	12.44	20
Outer lip	f	8.68	0.15	8.49	8.98	4	9.45	0.28	8.75	9.98	17
Outer lip	m	8.01	0.26	7.41	8.41	6	8.98	0.28	8.42	9.87	20
Last whorl	f	9.70	0.24	9.43	10.08	4	10.61	0.28	9.84	11.47	17
Last whorl	m	8.90	0.13	8.65	9.09	6	9.97	0.25	9.54	10.66	20
Col. axis	f	8.67	0.16	8.49	8.99	4	9.59	0.32	8.86	10.66	17
Col. axis	m	8.05	0.09	7.93	8.17	6	8.95	0.29	8.13	9.78	20
Weight	f	0.200	0.030	0.175	0.260	4	0.259	0.036	0.142	0.344	17
Weight	m	0.200	0.034	0.130	0.238	6	0.249	0.040	0.131	0.331	20
Volume	f	0.574	0.030	0.542	0.624	4	0.703	0.050	0.548	0.820	16
Volume	m	0.432	0.036	0.371	0.494	6	0.562	0.038	0.452	0.686	19

"Río Barbilla" (altitude 70 m) lot IR 1545							"Uatsi" (altitude 30 m) lots IR 766, IR 1114, IR 1632				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	12.22	0.00	12.21	12.22	2	12.61	0.18	12.28	12.79	6
Height	m	11.32	0.50	10.75	12.12	5	11.94	0.18	11.59	12.15	5
Maj. diam.	f	13.93	0.00	13.93	13.93	2	14.04	0.15	13.78	14.33	6
Maj. diam.	m	12.73	0.47	11.97	13.61	5	13.36	0.60	12.64	14.35	5
Min. diam.	f	12.60	0.02	12.58	12.62	2	12.68	0.19	12.45	12.97	6
Min. diam.	m	11.37	0.43	10.73	12.09	5	12.05	0.44	11.52	12.98	5
Outer lip	f	9.29	0.02	9.27	9.30	2	9.50	0.19	9.16	9.95	6
Outer lip	m	8.57	0.29	8.04	8.95	5	9.19	0.35	8.32	9.68	5
Last whorl	f	10.31	0.10	10.21	10.41	2	10.51	0.20	10.04	10.81	6
Last whorl	m	9.60	0.45	8.78	10.30	5	9.98	0.30	9.56	10.57	5
Col. axis	f	9.41	0.25	9.16	9.66	2	9.53	0.12	9.36	9.81	6
Col. axis	m	8.62	0.35	8.11	9.32	5	8.89	0.16	8.71	9.11	5
Weight	f	0.240	0.012	0.228	0.251	2	0.263	0.036	0.219	0.335	6
Weight	m	0.157	0.041	0.089	0.219	5	0.148	0.049	0.087	0.226	5
Volume	f	0.688	0.019	0.669	0.707	2	0.708	0.021	0.681	0.744	6
Volume	m	0.547	0.073	0.442	0.695	5	0.631	0.074	0.546	0.764	5

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"Shiroles" (altitude 100 m) lots IR 911, IR 1596, IR 1599, IR 1644							"Cahuita" (altitude 0–10 m) lots IR 107, IR 757, IR 897, IR 898, IR 907, IR 1095, IR 1312, IR 1555, IR 1557, IR 1630, IR 1639, IR 1648				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	12.54	0.57	11.97	13.10	2	11.31	0.53	10.21	12.73	63
Height	m	12.04	0.30	11.67	12.50	4	10.66	0.54	9.20	12.08	51
Maj. diam.	f	14.16	0.63	13.53	14.79	2	12.76	0.52	11.59	14.55	63
Maj. diam.	m	13.49	0.25	13.14	13.82	4	12.26	0.53	10.85	14.43	51
Min. diam.	f	12.81	0.29	12.52	13.10	2	11.67	0.46	10.62	13.26	63
Min. diam.	m	12.21	0.19	11.82	12.41	4	11.04	0.45	9.88	12.67	51
Outer lip	f	9.24	0.06	9.18	9.30	2	8.63	0.41	7.76	9.89	63
Outer lip	m	9.16	0.21	8.76	9.48	4	8.37	0.41	7.39	9.73	51
Last whorl	f	10.63	0.40	10.22	11.03	2	9.56	0.47	8.44	10.71	63
Last whorl	m	10.27	0.13	10.10	10.45	4	9.05	0.44	8.17	10.19	51
Col. axis	f	9.53	0.30	9.23	9.82	2	8.68	0.43	7.93	9.91	63
Col. axis	m	9.24	0.15	9.07	9.49	4	8.12	0.41	7.11	9.18	51
Weight	f	0.298	0.030	0.268	0.328	2	0.134	0.026	0.077	0.224	63
Weight	m	0.292	0.014	0.274	0.306	4	0.141	0.039	0.057	0.282	51
Volume	f	0.718	0.060	0.658	0.777	2	0.564	0.070	0.437	0.817	60
Volume	m	0.622	0.025	0.572	0.656	4	0.471	0.058	0.329	0.662	51

"Manzanillo" (altitude 0–10 m)						
lots IR 1096, IR 1320, IR 1642						
		Mean				
Sex		value	Deviation	Min	Max	Number
Height	f	11.81	0.43	10.43	12.45	10
Height	m	11.17	0.34	10.44	12.45	19
Maj. diam.	f	13.43	0.43	12.39	14.43	10
Maj. diam.	m	12.79	0.45	12.01	13.70	19
Min. diam.	f	12.11	0.40	11.25	12.96	10
Min. diam.	m	11.48	0.33	10.99	12.25	19
Outer lip	f	9.11	0.47	7.97	9.76	10
Outer lip	m	8.66	0.28	8.03	9.23	19
Last whorl	f	9.97	0.33	9.28	10.55	10
Last whorl	m	9.31	0.24	8.79	10.03	19
Col. axis	f	8.93	0.34	7.91	9.57	10
Col. axis	m	8.56	0.27	7.96	9.29	19
Weight	f	0.180	0.018	0.132	0.217	10
Weight	m	0.168	0.031	0.128	0.257	19
Volume	f	0.615	0.053	0.486	0.719	10
Volume	m	0.522	0.043	0.452	0.630	19

still lacking their thickened outer lip but otherwise being fully grown weigh from approx. 50 to 100 mg depending on the size, with adults ranging up to 344 mg. Thus, the weight is mainly influenced by the thickness of the outer lip, which not only depends on the age of the individual but also on size. A recently devel-

oped outer lip is probably thinner than the one of a truly fully grown individual, a factor that cannot be differentiated in field collections, although the attempt was made to at least exclude non fully grown adult shells in populations with sufficient material. The arrows in the figure exemplary indicate such

"thin-lipped" adults. In fact, this may have resulted in too low measurements, thereby reducing the mean value.

In the diagrams, the populations are roughly grouped according to their locations: Rincón de la Vieja to Monteverde (NW-Costa Rica: mountain chains of Guanacaste and Tilarán), Las Pavas to La Selva (western and northern Caribbean plain), Guayacán to Barbilla (middle Caribbean plain), and Uatsi to Manzanillo (southern Caribbean plain).

Because the sex of the additional populations from the INBio material could not be determined, they have to be compared to the average value of both sexes.

Morphometry: The comparison of the populations showed that they differ in all characteristics. Except for weight, these differences between the populations exhibit a similar pattern in each characteristic (Figs. 21–28); that is, "Monteverde – Finca Ecológica" always has the smallest dimensions, suggesting that relations between the measurements at each locality are constant. In fact, several relations were tested and, except for the size, no significant differences were found at the different locations. The individual data can diverge remarkably from the mean value and as may be expected, due to the fact that as more specimens are

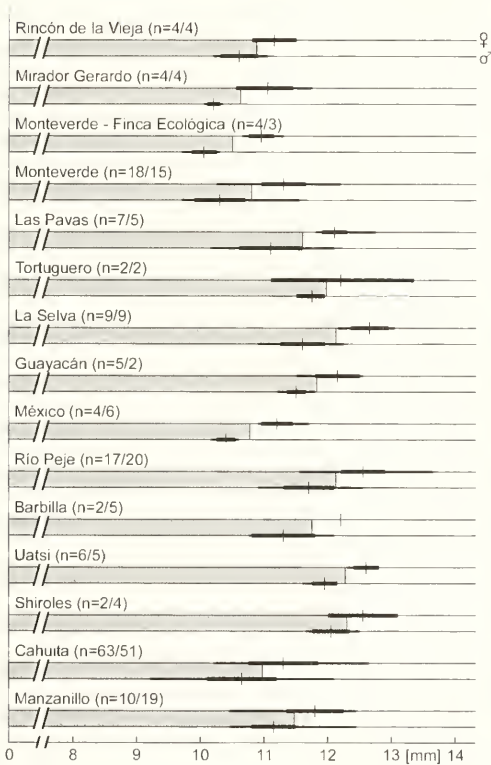


FIG. 21. Shell height of different populations of *Helicina funcki* in Costa Rica according to Table 3; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males"; upper line: females, lower line: males; in between and shaded: average of both for comparison with populations of unknown sex.

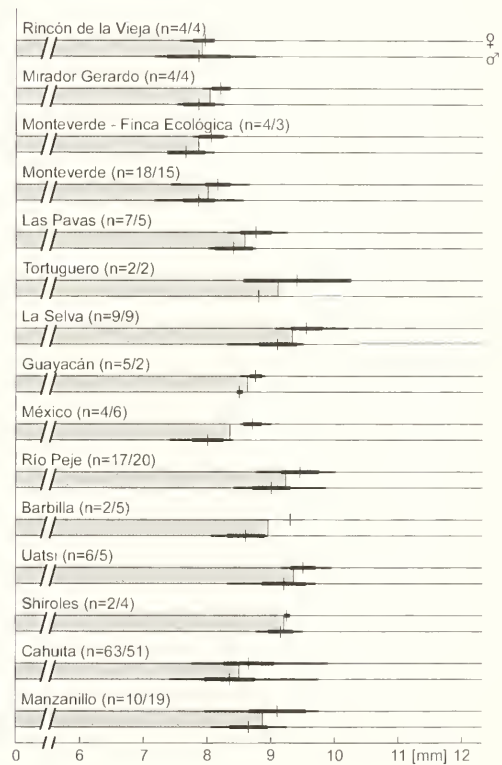


FIG. 22. Expansion of outer lip of different populations of *Helicina funcki* in Costa Rica according to Table 3; for explanations see Fig. 21.

included in the investigation, the wider the range of the data can become. Regarding these size differences, the volume appears to illustrate them best, especially because it is the only measurement directly reflecting the actual living conditions of the animal. The extrema: the biggest individual from Tortuguero (0.865 ml) had a shell with 2.75 times the volume of the smallest from Monteverde – Finca Ecológica (0.315 ml); the mean value of the population of Shiroles is 1.7 times higher than that of Monteverde – Finca Ecológica. At the upper four locations in Fig. 27 (mountain chains of Guanacaste and Tilarán), representing the highest altitudes, consistently smaller-shelled populations are found, as well as at two far distant localities in the Caribbean plain (México and Cahuita). Shells from Las

Pavas, Guayacán and Manzanillo are of intermediate size (Fig. 29). Additional populations from the collection of INBio were subsequently compared only in the minor diameter, because the volume could not be measured and – as previously demonstrated – other characteristics varied in the same way. The minor diameter was chosen instead of the height, because it can be measured more exactly and it is better correlated with the volume (Fig. 30, Cahuita population). The populations show similar differences in size at different sites (Figs. 24, 29). The two individuals of Isla Uvita represent the smallest *Helicina funcki* measured in this study. The few corresponding localities (Monteverde, Manzanillo, Rincón de la Vieja, Mirador Gerardo – Santa Elena, Shiroles close to Hitoy Cerere) agree sur-

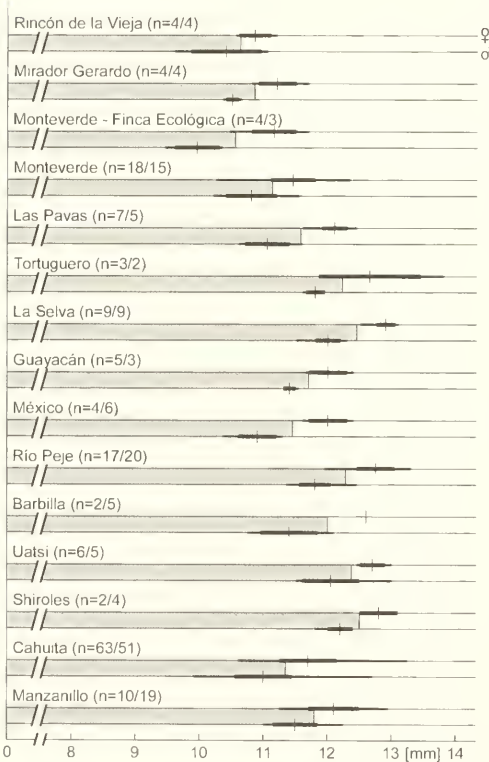


FIG. 23. Minor diameter of shell of different populations of *Helicina funcki* in Costa Rica according to Table 3; for explanations see Fig. 21.

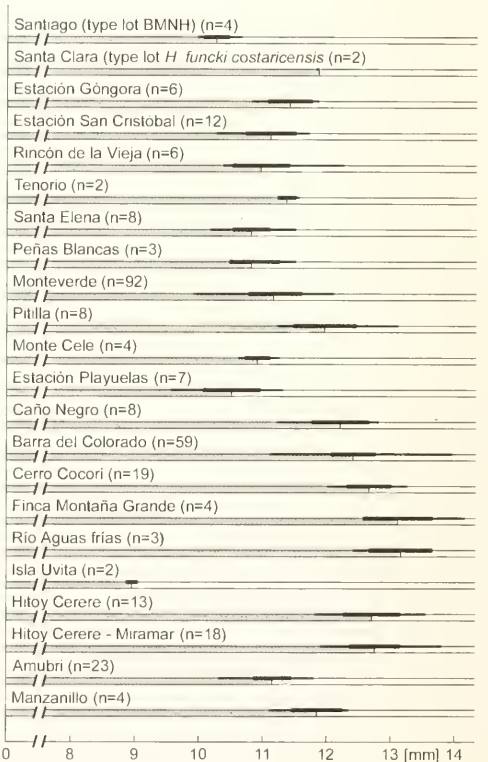


FIG. 24. Minor diameter of shell of different populations of *Helicina funcki* in Costa Rica, INBio collection, according to Table 4, and type material of *Helicina funcki* and *Helicina funcki costaricensis*; for explanations see Fig. 21.

prisingly well in their mean values, although this is often not supported by very extensive data in my own material or INBio's, respectively. This even agrees with the results of the analysis of "non-statistical" numbers of specimens.

Following up the fact that the highest localities always had the small-shelled populations, the average minor diameter of the 34 populations (Isla Uvita excluded) was plotted against the elevation (Fig. 31). A constant decline of the maximum values with increasing elevation is clearly visible, suggesting an influence by elevation. Furthermore, all the data scattered below this decline in maximum size indicate that altitude is not the only important parameter. The range of possible influences is too wide, and *Helicina funcki*, although widely distributed, occurs at

very scattered locations so that very detailed and local studies of environmental conditions would be required to trace any further correlation.

Sexual Dimorphism: Besides weight, females in all measurements and in all populations are clearly bigger than males, although the range of measurements overlaps widely, as exemplified for Cahuita by the minor diameter-height-relation (Fig. 32). Even with a small sample size of sometimes as few as two individuals, this result is always confirmed. Furthermore, the range of the differences is often about the same as in the more extensively supported data of the populations from Cahuita, Río Peje and Monteverde. The males have a volume of about 81% of females.

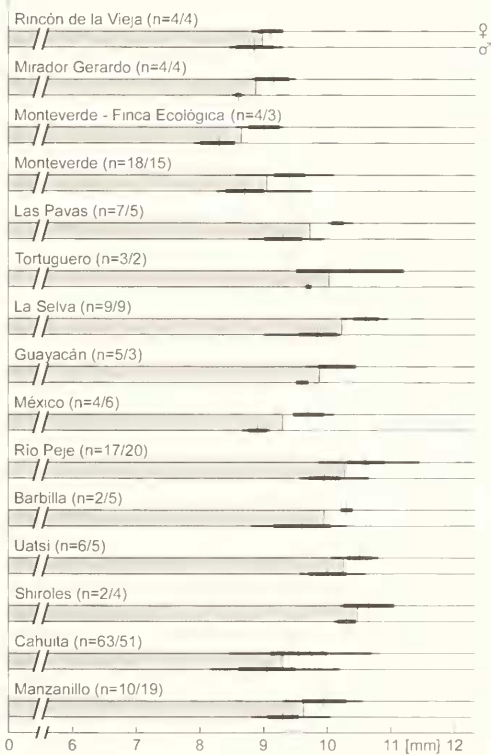


FIG. 25. Height of last whorl of different populations of *Helicina funcki* in Costa Rica according to Table 3; for explanations see Fig. 21.

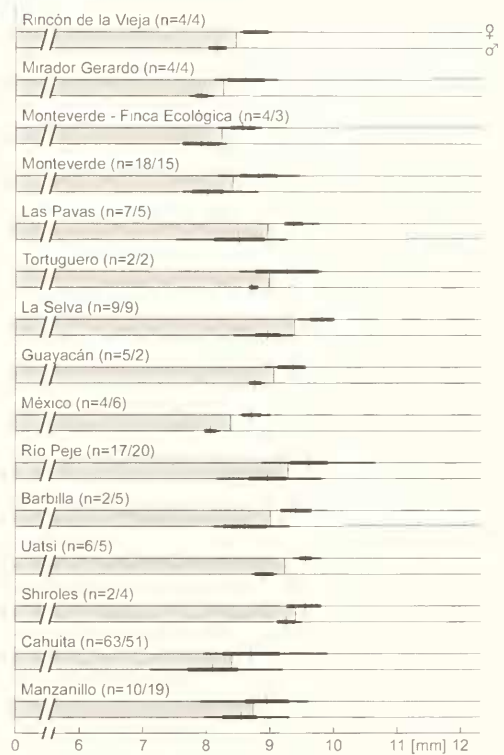


FIG. 26. Height of columellar axis of different populations of *Helicina funcki* in Costa Rica according to Table 3; for explanations see Fig. 21.

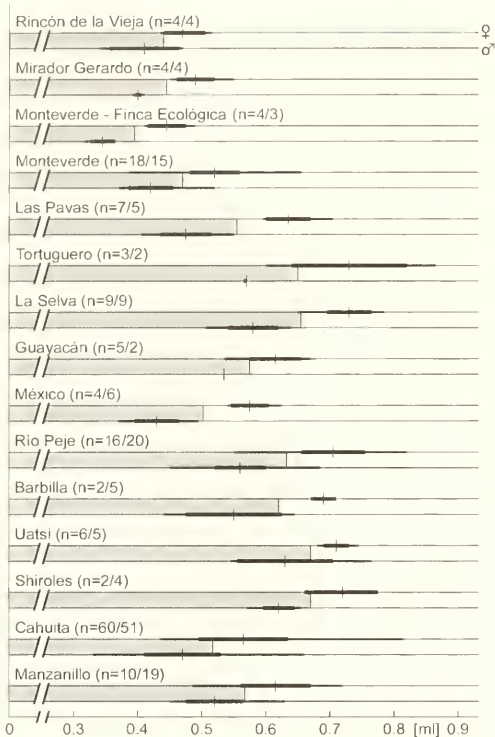


FIG. 27. Shell volume of different populations of *Helicina funcki* in Costa Rica according to Table 3; for explanations see Fig. 21.

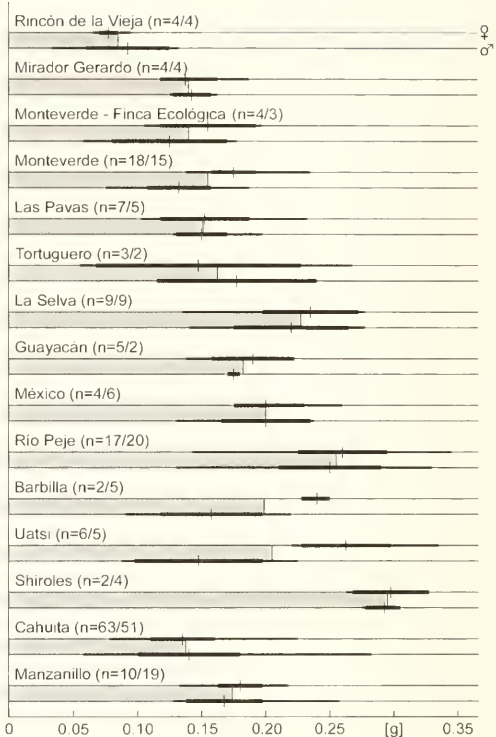


FIG. 28. Shell weight of different populations of *Helicina funcki* in Costa Rica according to Table 3; for explanations see Fig. 21.

TABLE 4. Minor diameter measurements [mm] of different populations of *Helicina funcki* from the INBio collection and type material, given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens.

Locality	Mean value	Devi- ation	Min	Max	Number	Lots
Santiago (type lot BMNH)	10.24	0.22	9.95	10.67	4	BMNH 20010497.1-4
Santa Clara (type lot <i>H. funcki costaricensis</i>)	11.84	0.02	11.82	11.86	2	MIZ 8989
Estación Góngora	11.42	0.34	10.80	11.85	6	INBio 1480300, 1480475, 1483409, 1484993, 1488083
Estación San Cristóbal	11.09	0.38	10.26	11.68	12	INBio 1488065, 1498494
Rincón de la Vieja	10.95	0.47	10.34	12.27	6	INBio 1466644, 1487945, 1498739, 1498744
Tenorio	11.37	0.17	11.20	11.54	2	INBio 1485411, 1498593
Santa Elena	10.81	0.30	10.13	11.48	8	INBio 1498638

(Continues)

(Continued)

Locality	Mean value	Devi- ation	Min	Max	Number	Lots
Peñas Blancas	10.82	0.44	10.45	11.48	3	INBio 1480605, 1498802
Monteverde	11.13	0.45	9.89	12.08	92	INBio 1466835, 1466842, 1466863, 1466870, 1466884, 1466891, 1466905, 1466912, 1466954, 1467003, 1467010, 1467031, 1468211, 1477521, 1477749, 1479517, 1479528, 1479539, 1479550, 1480098, 1480119, 1480126, 1480127, 1480128, 1480129, 1480130, 1480131, 1480132, 1480149, 1480152, 1480426, 1484687, 1485422, 1485426, 1485441, 1498581, 1498590, 1498632, 1498804, 1498806, 1498807, 1498828
Pitilla	11.94	0.49	11.22	13.08	8	INBio 1463787, 1463946, 1480043, 1480289, 1480318, 1480319
Monte Cele	10.91	0.22	10.58	11.26	4	INBio 1488042
Estación Playuelas	10.49	0.44	9.53	11.32	7	INBio 1479506, 1487809, 1498571
Caño Negro	12.20	0.47	11.18	12.78	8	INBio 1466940, 1480029, 1487043, 1487611, 1487878, 1501040
Barra del Colorado	12.39	0.35	11.09	13.97	59	INBio 1465700, 1477915, 1478017, 1478283, 1478294, 1480041, 1480051, 1484010, 1484013, 1484372, 1484374, 1484585, 1484587, 1484589, 1484748, 1484749, 1484991, 1485145, 1485284, 1485285, 1485289
Cerro Cocorí	12.67	0.34	11.98	13.25	19	INBio 1465446, 1467174, 1478061, 1480255, 1480261, 1483017, 1483208, 1483360
Finca Montaña Grande	13.08	0.53	12.53	14.15	4	INBio 1498610, 1501098
Río Aguas frías	13.16	0.50	12.41	13.66	3	INBio 1487980
Isla Uvita	8.95	0.09	8.86	9.03	2	INBio 3315386
Hitoy Cerere	12.72	0.44	11.82	13.55	13	INBio 1463392, 1466444, 1473832, 1475438, 1476246, 1476262, 1497862, 1497905, 3091789
Hitoy Cerere - Miramar	12.73	0.39	11.91	13.81	17	INBio 1475234, 1475694, 1475720, 1475725, 1475930, 1476376, 1476490, 1476687, 1476688, 1480272
Amubri	11.13	0.28	10.32	11.81	24	INBio 1467294, 1477569, 1477585, 1483302, 1483381, 1483382, 1483386, 1483387, 1483389, 1483390, 1483392, 1483394, 1483398, 1483400, 1483407, 1485365, 1485382, 1493444
Manzanillo	11.86	0.39	11.08	12.33	4	INBio 3097895, 3097906

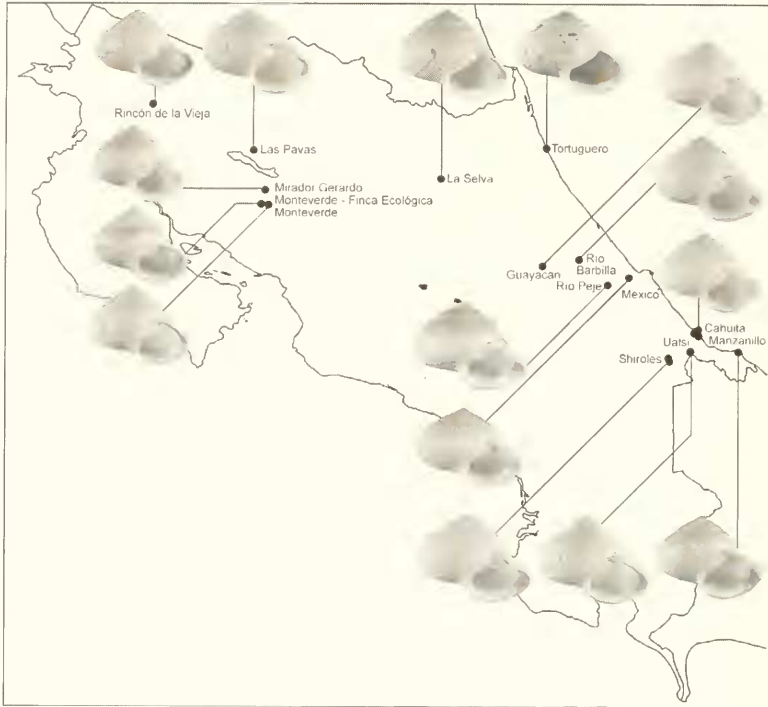


FIG. 29. Size variations in Costa Rican populations of *Helicina funcki*: shell height in figures reflects the mean value of the respective females; each shell originates from the respective locality and is randomly chosen according to the approximation of the mean value.

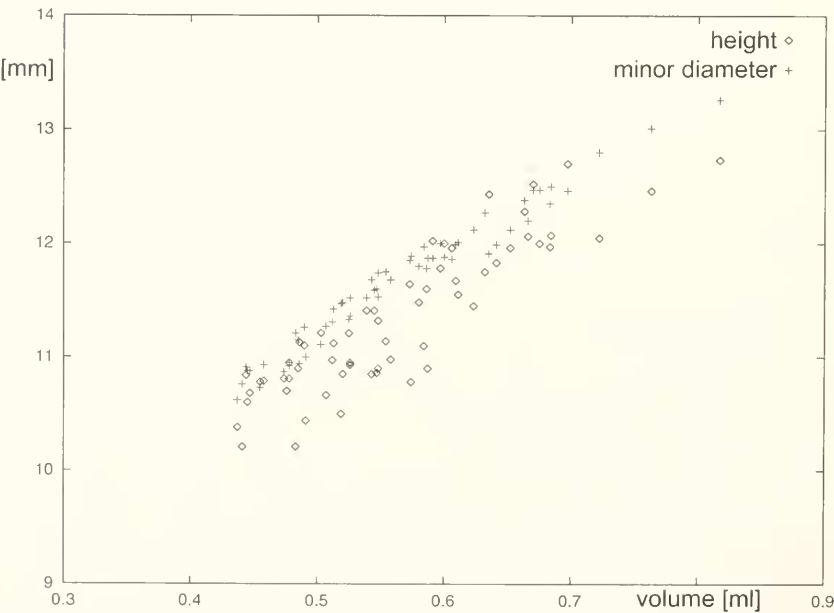


FIG. 30. Relation of shell height and minor diameter respectively to the volume in *Helicina funcki* exemplary for the females of the population from Cahuita.

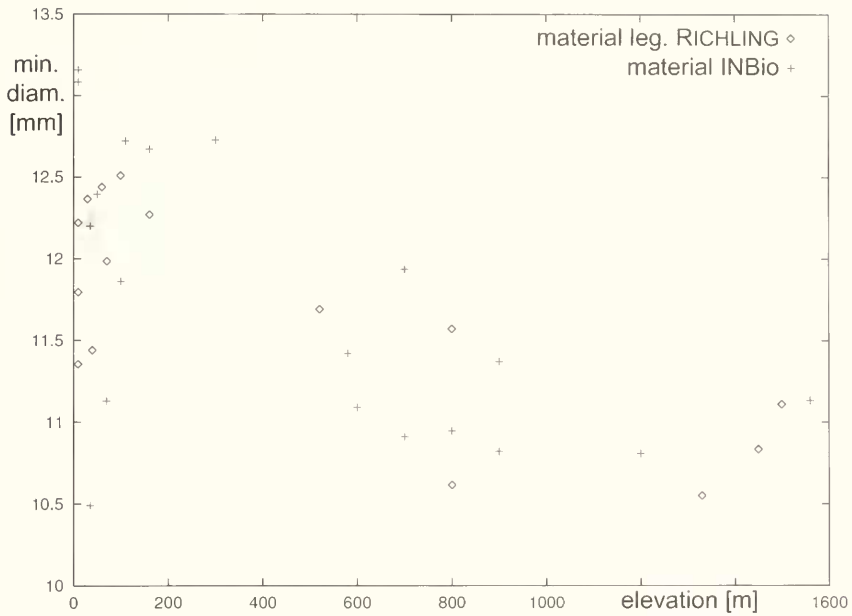


FIG. 31. Relation of minor diameter of shell to elevation of locality of different populations of *Helicina funcki* in Costa Rica; sex-independent mean values were used.



FIG. 32. Range of measurements in females and males exemplary for height and minor diameter in the population from Cahuita.

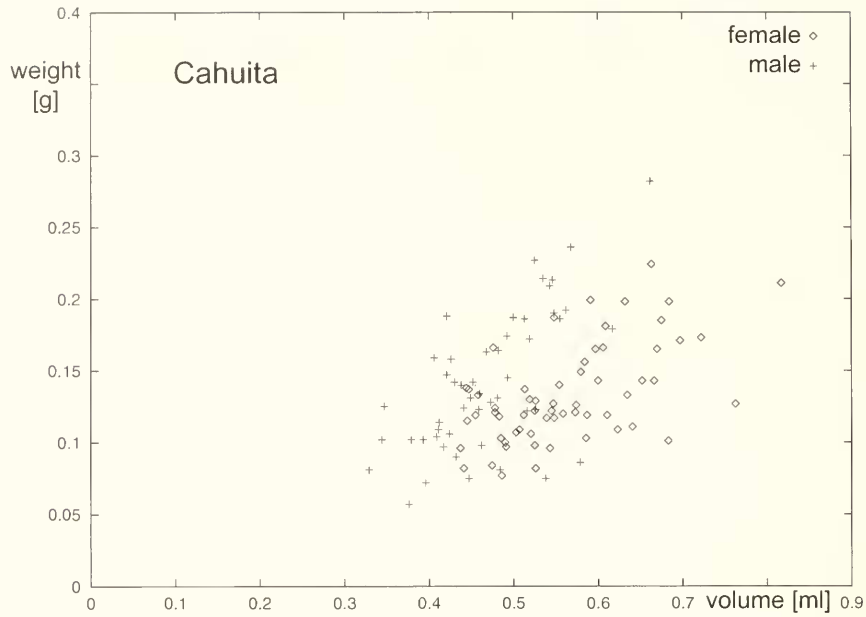


FIG. 33. Relation of weight to volume in females and males of the population of *Helicina funcki* from Cahuita (material according to Table 3).

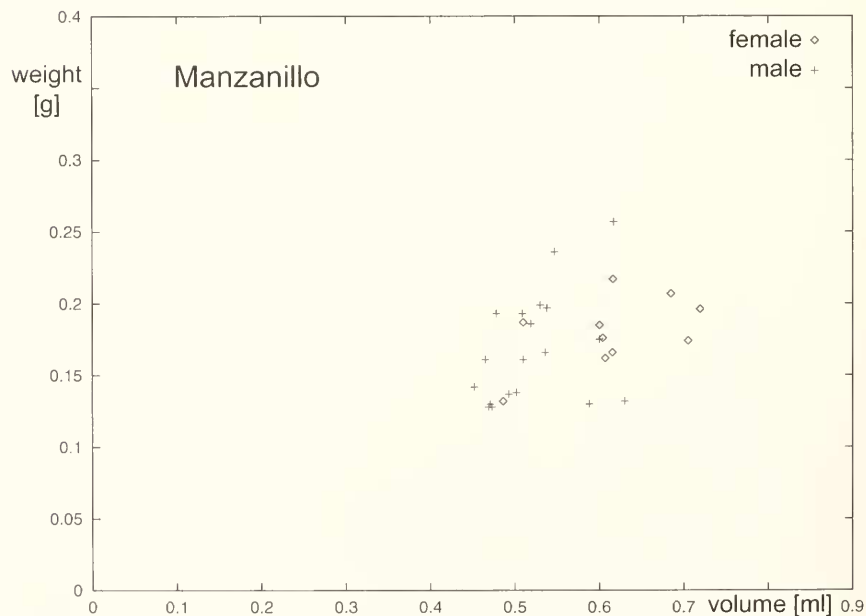


FIG. 34. Relation of weight to volume in females and males of the population of *Helicina funcki* from Manzanillo (material according to Table 3).

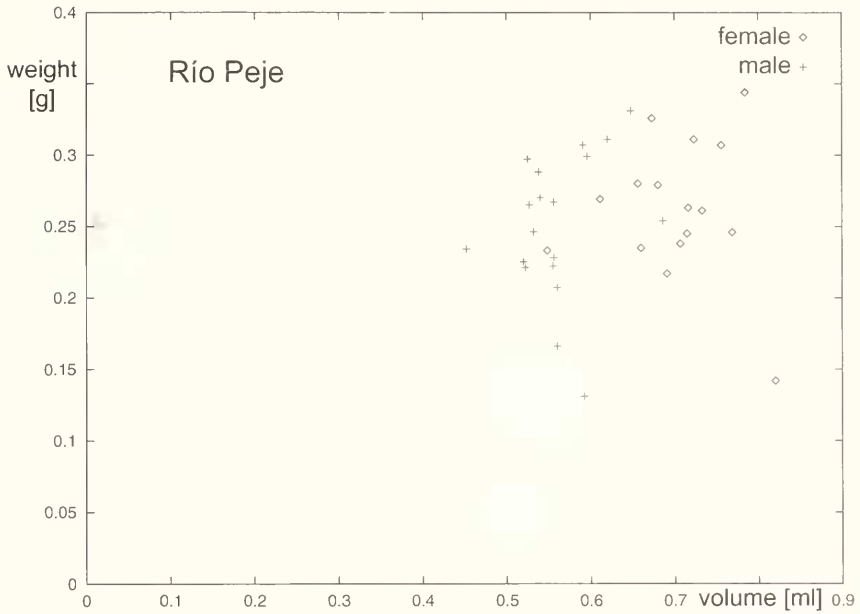


FIG. 35. Relation of weight to volume in females and males of the population of *Helicina funcki* from Río Peje (material according to Table 3).

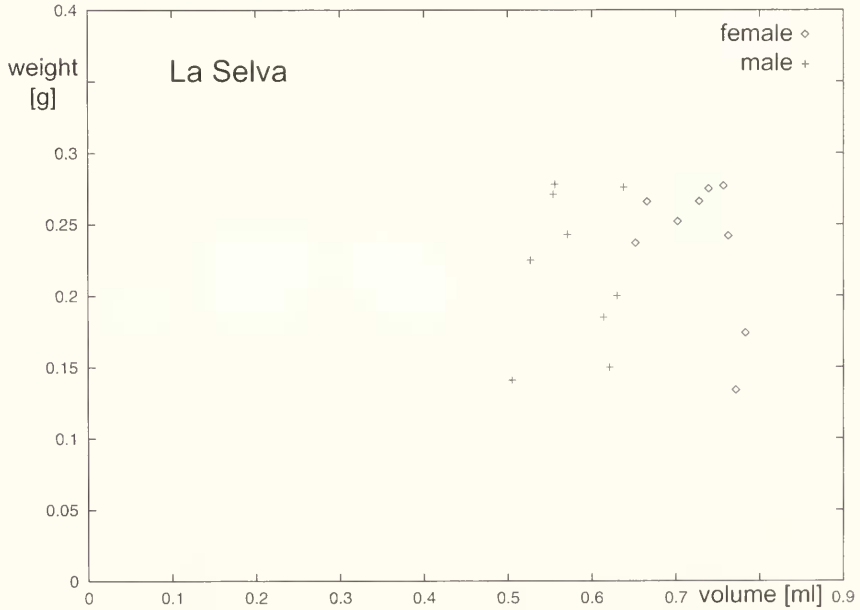


FIG. 36. Relation of weight to volume in females and males of the population of *Helicina funcki* from La Selva (material according to Table 3).

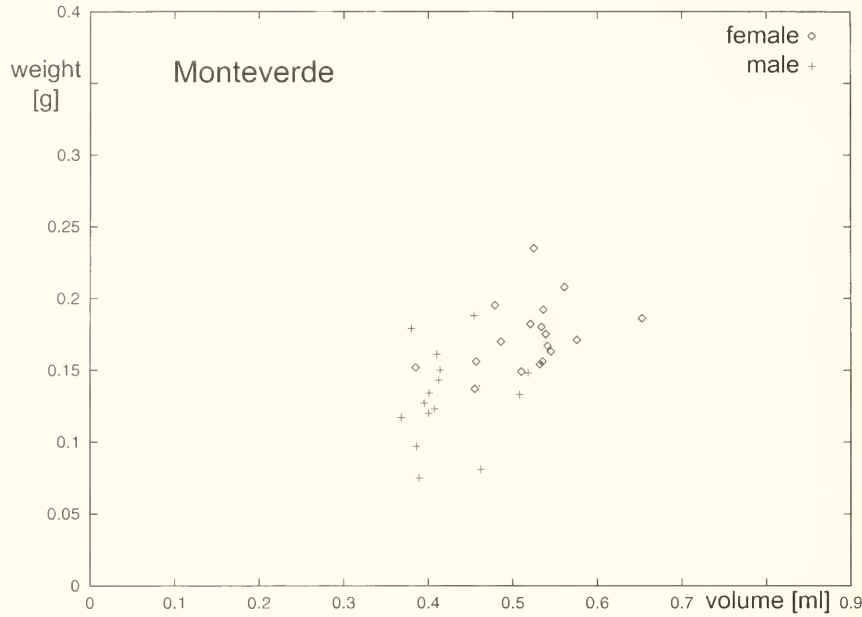


FIG. 37. Relation of weight to volume in females and males of the population of *Helicina funcki* from Monteverde (material according to Table 3).

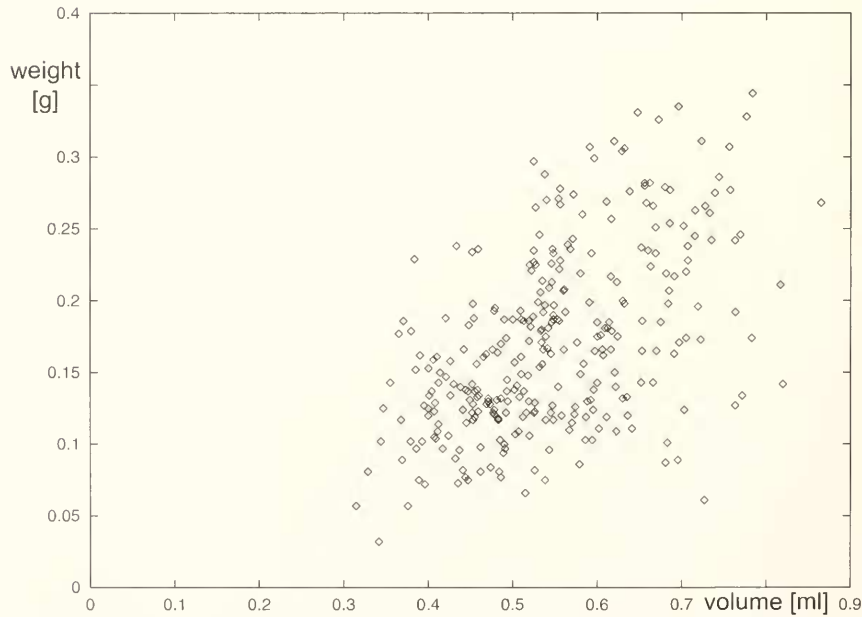


FIG. 38. Relation of weight to volume in adults of *Helicina funcki* in Costa Rica (all material listed in Table 3 included).

Considering the problems connected with the weight measurements, the data (Fig. 28) indeed show contrary results even in otherwise rather similar populations (e.g., upper rows: Rincon de la Vieja to Monteverde). When only looking at the better-supported data – namely Monteverde, La Selva, Rio Peje, Cahuita, Manzanillo – the difference between males and females is greater in the population at Monteverde than in La Selva, Rio Peje and Manzanillo, whereas at Cahuita this relationship is even reversed. Taking into account the greater size of all females, it seems that in the lowland populations the males invest more material in their shells than females of the same volume do. To test this assumption, the relation of weight to volume is plotted for these populations (Figs. 33–37). Because the mathematical relation between weight and volume is unknown and males and females fall into a different range, the data of all specimens of *Helicina funcki* used in the morphometric analysis were plotted as an adjustment for comparison (Fig. 38). As expected, the latter measurements are widely scattered, but a linear approximation or a function of greater degree would better match the data. A higher volume should result in a higher weight. The Monteverde population clearly demonstrates this relation for both sexes (Fig. 37), whereas the males of the lowland populations on average weigh the same as females with a higher volume (Figs. 33–36). For other localities, the deviations explained above seem to be interposed with the actual results.

Habitat

Biolley (1897) found the species on the trunks of trees, the stems of plantains (*Musa*) and also on the ground. Except for the last habitat, these observations could be confirmed during the field work for this study. Moreover, *Helicina funcki* often crawls and aestivates on the underside or more seldom on the upper side of different kind of leaves. The recognized plants belong not only to Musaceae, Heliconiaceae, and palms, but also to various herbs of the undergrowth. *Helicina funcki* may even be found on climbing species such as the Araceae *Monstera* spec. Probably because of the relatively large size of the species, it is found on plant species with

large leaves. But it lives on trunks, branches and twigs of trees, bushes and tree ferns as well. *Helicina funcki* not only crawls on live leaf surfaces, it was also found in the dead, dried and curled-up leaves, especially those of bananas. In areas of human influence specimens were observed on concrete walls of buildings or wooden fences. Thus, *H. funcki* is a typical arboreal species, having been observed up to 7 m or more above the ground. With regards to alimentation, it was definitely found feeding on the surface of trunks and on living and dead leaves.

Distribution

Helicina funcki is confined to southern Central America. Although for Nicaragua it has thus far only been recorded by Ancey (1897) from Greytown at the mouth of the Rio San Juan, with a further unspecified lot in the collection of the UF and a site somewhere along the southern border of the Rio San Juan (von Martens, 1901), the distribution range extends at least from southern Nicaragua to the Canal Zone in Panama. It most probably occurs in the eastern Caribbean lowlands further north in Nicaragua as well, because the habitats do not change greatly. Furthermore, the wide distribution in northern Costa Rica and the morphometric data suggest that in this area *H. funcki* has not come close to its distribution limit.

Due to the lack of literature records for the better investigated countries, such as Honduras, Guatemala and Belize, and due to the absence of *H. funcki* in the extensive Central American collection of the UF (checked personally) any occurrences north of Nicaragua can be excluded. The relatively large size furthermore renders the species unlikely to be overlooked. The records from Ylalag (Mexico: Oaxaca) by Wagner (1910a) therefore seems very questionable.

In Costa Rica, the species is fairly widely distributed throughout the Caribbean plain and on the mountain slopes (Fig. 39). The distribution is mainly influenced by the central mountain chains subdividing the country. *Helicina funcki* crosses the northern volcanic mountains (Cordillera de Guanacaste and Tilarán, Cordillera Central), where the upper Pacific slopes are connected to the Caribbean side by various valleys between the separate volcanoes. According to the present data, the species is known to occur up to 1,800 m. A limitation by altitude is furthermore supported

by the decline of the shell size with increasing elevation of the localities. In fact, the southern Cordillera de Talamanca, highly elevated as a continuous mountain chain (approximately 3,000 m), forms a clear barrier in the distribution of *H. funcki*. The exact occurrence on the Caribbean slope of this Cordillera is known only fragmentarily because the area is difficult to reach and has not been investigated. Continuing downhill towards the northern Pacific and in the Valle Central the climate becomes drier (Figs. 2, 3), therefore appearing to be the most important factor limiting the distribution. Except for the most southern Caribbean plain, *H. funcki* does not occur in areas of less than 2,000 mm annual precipitation. On the more humid southern Pacific plains and slopes, *H. funcki* is replaced by *H. pitaisensis*.

The single record of *H. funcki* on the Peninsula de Osa (INBio 1486976) seems to contradict the otherwise continuous distribution. Upon request, the data were confirmed by INBio. The specimen is small (9.4/12.1/9.5

mm). There is no reason to question the finding, despite the fact that several collecting efforts of INBio up to now have yielded only one specimen, because species of Helicinidae are extremely rare on Peninsula de Osa.

Biolley in 1897 reports the species as the most common land snail of the country. Nowadays due to the extreme change of the land use (e.g., deforestation in large areas), it probably will be shown that synanthropic snails like *Subulina octona* (Bruguière, 1789), the introduced *Ovachlamys fulgens* (Gude, 1900) (Barrientos, 2000) and *Succinea costaricana* von Martens, 1898, the latter known as pest species in agriculture (Villalobos et al., 1995), are now much more common.

Discussion

The differences of *Helicina funcki costaricensis* to the nominal species mentioned by Wagner (1910a) can be summarized as differences in size and in a more strongly

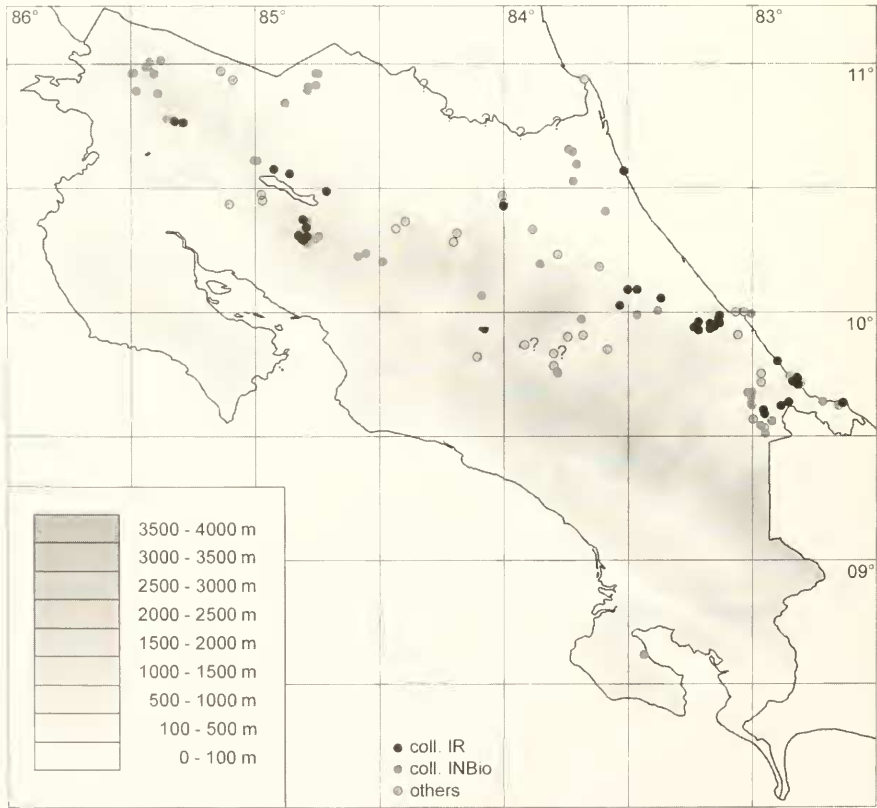


FIG. 39. Records of *Helicina funcki* in Costa Rica.

developed outer lip. The original description of the subspecies does not include any comparison with *H. funcki*. Astonishingly, Wagner (1910a) gives higher dimensions (12–15/15–18/12–14 mm) than in his publication in 1905 (11.0/13.3/11.3 mm), which on one hand clearly are exaggerated, on the other hand the indeed higher values from specimens from San José were most likely included in his measurements. The morphometric investigations of different populations of *H. funcki* suggest that the size depends on environmental factors and is not suitable for the separation of a subspecies in absence of other differentiating characters. The type lots of both the nominal form and the subspecies fall in the range of the Costa Rican specimens (Fig. 24). *Helicina funcki* reaches maximum sizes in lowlands to which the type locality of *H. funcki costaricensis* belongs. The nominal species is described from close to the southern limit of its distribution (Fig. 39), which makes it likely that environmental conditions of this area are less favorable for the species, such as perhaps at high elevations, which may result in smaller shells. Therefore, *H. funcki costaricensis* is regarded as a synonym of *H. funcki*. Regarding the comparably large shells mentioned by Wagner (1905, 1910a) (checked: MIZ 8990: 2 ads.: 13.4/16.0/13.2 mm; 13.9/15.7/12.9 mm) from San José, the locality given without comment is misleading, because one would immediately think of San José, capital of Costa Rica (in the historical times of Wagner a possible locality). But considering the relation of shell size to elevation of the locality (Fig. 31), the site appears to be in contradiction to the shell size because San José is located at about an altitude of 1,160 m. Biolley (1897) reported a small form of *H. funcki* from Cartago (close to San José, at a similar elevation). A closer examination of the map of Costa Rica reveals a second San José in the Alajuela Province, close to Santa Clara, which is here suggested to be the locality “San José”. It also supports the localization of “Santa Clara”. Under *H. funcki costaricensis*, Wagner (1910a) mentions a somewhat dubious form from Ylalag, Mexico in his collection, which is said to be more elevated and remarkably angulated at the periphery. It could not be checked and therefore cannot be discussed any further, especially because of the outstanding locality for *Helicina funcki*.

The description of *Helicina deppeana parvidens* has to be discussed in the context

of material in the ZMB. *Helicina deppeana* von Martens, 1863, was described from Mexico (locality unknown) and was figured later (von Martens, 1865, 1890) together with a variety from Yalalag (State of Oaxaca, Mexico). The study of the original material of the figures stored in the ZMB revealed the following: the typical *H. deppeana* (syntypes ZMB 4571) are not conspecific with *H. funcki*, for example, they do not have the typical ornamentation of lighter patches, and are more solid and unicolored. The specimens of the variety from Yalalag (ZMB 1743) look exactly like specimens of *H. funcki* and thus are specifically different from *H. deppeana*, an observation already remarked on the label by Wagner: “nach meiner Ansicht stellen die vorliegenden Exemplare nur *Helicina funcki* dar” [= in my opinion the specimens only represent *H. funcki*]. Interestingly, Wagner (1910a) completely avoids any comment on this in his monograph, although it is certain that he had seen the collection prior to his publication, because various types of newly described species (e.g., *H. pitalensis*, *H. tenuis pittieri*) are in the ZMB collection. The singular Mexican locality of *H. funcki* is discussed in the paragraph “Distribution”. Returning to *H. deppeana parvidens*, it is very likely that when Pilsbry (1920a) published his work on Costa Rican land molluscs, he used the Biologia Centrali-Americana (von Martens, 1890–1901), representing the only comprehensive contribution for the area even today. It therefore appears probable that Pilsbry was misled by this figure and classified part of his Costa Rican material of *H. funcki* as a new subspecies of the Mexican *H. deppeana*.

Helicina (Tristramia) pitalensis
Wagner, 1910

Helicina funcki – von Martens, 1900: 603–604: Costa Rica: SW-Costa Rica: Bay of Terraba [mouth of Río Terraba, about 09°00'N, 83°36'W, Puntarenas Province], Tocori in the valley of the Río Paquita [NE of Quepos, canton Aguirre, 09°29'43"N, 84°04'52"W, 10 m a.s.l., Puntarenas Province], middle part of the Río Saveque [now: Río Savegre, about 09°29'N, 83°56'W, San José Province] and lower part of the Río Pacuare [now Río Pacuar south of San Isidro de El General [not Río Pacuare on Atlantic slope!], about 09°16'N, 83°39'W, San José Province] (Pittier); El Pital, in the valley of the Río

Naranjo [near Londres? (about 09°27'N, 84°05'W, Puntarenas Province), some specimens banded and others more elevated (Pittier) [in part] [non L. Pfeiffer, 1849] *Helicina pitalensis* Wagner, 1910a: 308, pl. 61, figs. 17–19

Helicina amoena – Monge-Nájera, 1997: 113: Costa Rica [non L. Pfeiffer, 1849]

Original Description

“Gehäuse kegelförmig mit gewölbter Basis, festschalig, leicht glänzend, zitrongelb mit undeutlichen weissen Flecken und Punkten, sowie einer schmalen rotbraunen Binde über der Naht und dem Kiel. Die Skulptur besteht aus feinen, etwas ungleichmässigen Zuwachsstreifen, auch erscheint die Epidermis unter der Lupe sehr fein gerunzelt. Das regelmässig spitzkegelförmige Gewinde besteht aus 5–5½ leicht gewölbten, langsam zunehmenden Umgängen, welche durch eine hell berandete, schwach eingedrückte Naht geschieden werden; der letzte ist beiderseits gleichmässig gewölbt, an der Peripherie deutlich kantig bis stumpf gekielt und steigt vorne nicht herab (unmittelbar vor der Mündung ein wenig hinauf). Die abgerundet dreieckige Mündung ist schief, innen gelb mit durchscheinender Binde. Der leicht verdickte, gelbliche Mundsaum erweitert; der Oberrand schmal und an der Insertion vorgezogen, der Aussen- und Basalrand breit umgeschlagen. Die kurze, abgerundete Spindel ist senkrecht oder leicht nach links gebogen; am Uebergange derselben in den Basalrand der Mündung eine zahnartig vorspringende Ecke. Der sehr dünne, feingekörnelte Basalkallus nur im Umkreise der

Spindel deutlich. Das Grübchen in der Nabelgegend undeutlich.

D = 14, d = 11,5, H = 13,5 mm.

Deckel birnförmig mit seitlich gekrümmter [sic] Spitze schwarzbraun bis pechschwarz mit lichterem Streifen entlang der Sigmakante; die dünne, feingekörnelte Kalkplatte nur am Spindelrande etwas leistenartig verdickt; in den übrigen Verhältnissen typisch.

Fundort: El Pital im Tale des Río Naranjo im südwestlichen Costa Rica. Da abgebildete Exemplar im k. Museum zu Berlin.

Von der ähnlichen *Helicina funcki* Pfeiffer unterscheidet sich vorstehende neue Art durch die lebhaftere Färbung mit deutlicher Binde, die glänzende Oberfläche mit deutlicheren Zuwachsstreifen, das höhere Gewinde mit deutlich gewölbten langsam und regelmässig zunehmenden Umgängen, den weniger erweiterten, aber deutlich kantigen bis stumpfgekielten letzten Umgang, sowie besonders die abweichenden Verhältnisse der Mündung und des Mundsaumes.”

Type Material

ZMB 103240 “El Pital, 200 m, III.1893, Vallée du Río Naranjo, leg. Madame Pittier de Fahega” (the lot contains one specimen) Because the original description refers to one specimen in the ZMB which matches the figure, it is the holotype (Fig. 40).

Dimensions:

Holotype: 13.0/12.5/14.0/11.2/9.1/10.6/10.0 mm

Type Locality

“El Pital im Tale des Río Naranjo im südwestlichen Costa Rica”; El Pital could not be



FIG. 40. *Helicina pitalensis*, holotype, ZMB 103240, height 13.0 mm; scale bar 5 mm.

localized on recent detailed maps. The Río Naranjo leads into the Pacific Ocean at the southern border of the Parque Nacional de Manuel Antonio, a little south of Quepos. By the elevation given in the data remaining with the original material, the type locality can be assumed to be located near Londres [about 09°27'N, 84°05'W], Puntarenas Province.

Examined Material

LEG. I. RICHLING

Puntarenas: S *San Vito*, Wilson Botanical Garden, Las Cruces, sendero a Río Jaba, 08°46'57"N, 82°57'40"W, 1,160 m a.s.l., 27.08.1999: (IR 1013); 28.08.1999: (IR 1016)

N Neily, road from Ciudad Neily to San Vito, open area with a few trees, 08°40'23"N, 82°56'44"W, 180 m a.s.l., N Neily, 23.03.1997: (IR 209)

Fila de Cal, road from Ciudad Neily to San Vito, S Campo Dos, burned area, 08°41'00"N, 82°56'29"W, 630 m a.s.l., 23.03.1997: (IR 191)

Fila Costeña, north of Bajo Bonito (locally called Llano Bonito), N of Río Claro, rain forest, 08°44'41"N, 83°02'09"W, 980 m a.s.l., 24.03.1997: (IR 221); 15.02.1999: (IR 579); 29.08.1999: (IR 1028); 06.03.2001: (IR 1485)

INBIO COLLECTION

Puntarenas: *Parque Nacional Corcovado*: *Estación Sirena*, 08°28'52"N, 83°35'32"W, 5 m a.s.l.: leg. Mario Chinchilla, 23.03.1995: 1 juv. (INBio 1485050); *Sendero los Espaveles*, *Sirena*, 08°28'49"N, 83°35'42"W, 0 m a.s.l.: leg. Annia Picado, 25.03.1995: 1 ad. (INBio 1482837); 1 ad. (INBio 1482842); *Sendero Espaveles*, 08°29'05"N, 83°35'29"W, 0 m a.s.l.: leg. Socorro Avila, 23.03.1995: 1 ad. (INBio 1482627); *Sendero Espaveles*, 08°29'22"N, 83°35'14"W, 0 m a.s.l.: leg. Billen Gamboa R., 03.12.1995: 1 ad. (INBio 1485173); *Estación Sirena*, *Sendero Las Ollas*, 08°28'47"N, 83°35'40"W, 5 m a.s.l.: leg. Alejandro Azofeifa, 25.03.1995: 1 juv. (INBio 1484670); *Estación Sirena*, *Sendero Las Ollas*, 08°28'57"N, 83°35'20"W, 20 m a.s.l.: leg. Francisco Alvarado, 25.03.1995: 1 s.ad. (INBio 1484221); *Sendero los Patos*, 3.5 km al N. de la *Estación Sirena*, 08°30'46"N, 83°35'56"W, 0 m a.s.l.: leg. Ramon Angulo, 26.08.1994: 1 juv. (INBio

1480506); *Río Pavo*, 08°30'51"N, 83°35'44"W, 20 m a.s.l.: leg. M. Madrigal, 03.04.1996: 2 ads. (INBio 3542542)

Reserva Forestal Golfo Dulce: *Cerro La Torre*, *Finca La Purruja*, 08°32'04"N, 83°25'53"W, 400 m a.s.l.: leg. Javier Quesada, 05.05.1994: 1 s.ad. (INBio 1477485); *Agujas*, *alrededores de la estación*, 08°32'13"N, 83°25'33"W, 300 m a.s.l.: leg. A. Berrocal, 01.11.1998: 1 ad. (INBio 3397130)

Fila Cal: 24 km de *San Vito* hacia *Ciudad Neily*, 08°41'36"N, 82°56'36"W, 780 m a.s.l.: 29.08.1995: 1 ad. (INBio 1485456); 29.08.1995: 1 s.ad., 1 juv. (INBio 3121204) (all leg. Marianella Segura); 24.5 km S en la *carretera de San Vito* hacia *Ciudad Neily*, 08°40'55"N, 82°56'23"W, 600 m a.s.l.: leg. Zaidett Barrientos, 21.11.1995: 1 juv. (INBio 1485120)

4.5 km NW de *Ciudad Neily*, Camino Paralelo al Río Caño Seco, Colectado en hojarasca en helechos, 08°40'50"N, 82°57'25"W, 180 m a.s.l.: leg. M. Chinchilla, 22.11.1995: 1 ad. (INBio 3542525)

Linda Vista, *Río Claro*: 3 km NE de la *Escuela de Llano Bonito*, 08°44'54"N, 83°02'04"W: 920 m a.s.l., leg. Socorro Avila, 24.03.1997: 1 s.ad., 1 juv. (INBio 1494393); 950 m a.s.l., leg. Alexander Alvarado Mendez, 15.02.1999: 1 s.ad., 1 juv. (INBio 3091134)

OTHER SOURCES

COSTA RICA

Alajuela: La Paz, Chemin du rivièrè Sarapiquí [not localized, near Isla Bonita?, about 10°15'30"N, 84°11'W], Biolley, ex Godet, 12.1892 received: 1 ad. (ZMB 45501)

Description

Shell (Fig. 335D–E): Conical-subglobose, solid, relatively large, slightly shiny to dull. Color: basic color lemon yellow, sometimes less bright, with slender reddish-brown band between sutures or suture and the periphery respectively, in some specimens very light or obsolete. On account of this band, the upper whorls may appear darker. The periphery is always lighter. As in *Helicina funcki*, the color is overlapped by fine white patches and lines giving the shell a special ornamentation. Surface textured with fine, irregular growth lines and oblique grooves of different individual orientation but of same general direc-

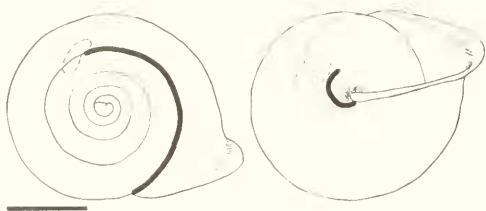


FIG. 41. Axial cleft and muscle attachments of *Helicina pitalensis*, IR 579; scale bar 5 mm.



FIG. 42. Teleoconch surface structure of *Helicina pitalensis*. A. On 2nd whorl. B. On 4th whorl; scale bar 100 μ m.



FIG. 43. Embryonic shell of *Helicina pitalensis*; scale bar 100 μ m.

tion (Fig. 42), causing the dull appearance. Embryonic shell with about 1 whorl; $4\frac{1}{8}$ – $4\frac{5}{8}$ subsequent whorls slightly convex; periphery remarkably angulated; whorls equally extending in size and slightly descending, only towards aperture slightly ascending; spire very regular. Suture slightly impressed and marginally lighter in color. Aperture oblique and nearly straight, inserting a little above periphery. Outer lip yellowish-whitish, very thickened, broadly expanded, only in the upper palatal part a little less strongly developed. Reflection nearly rectangular to

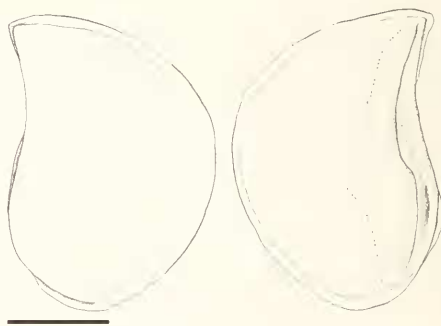


FIG. 44. Operculum of *Helicina pitalensis*, IR 579; scale bar 2.5 mm.

the whorl; transition to columella with a remarkably protruding denticle. Columella short, slightly curved, umbilical area without any groove or impressed line. Basal callus only close to columella present, thin, slightly granulated.

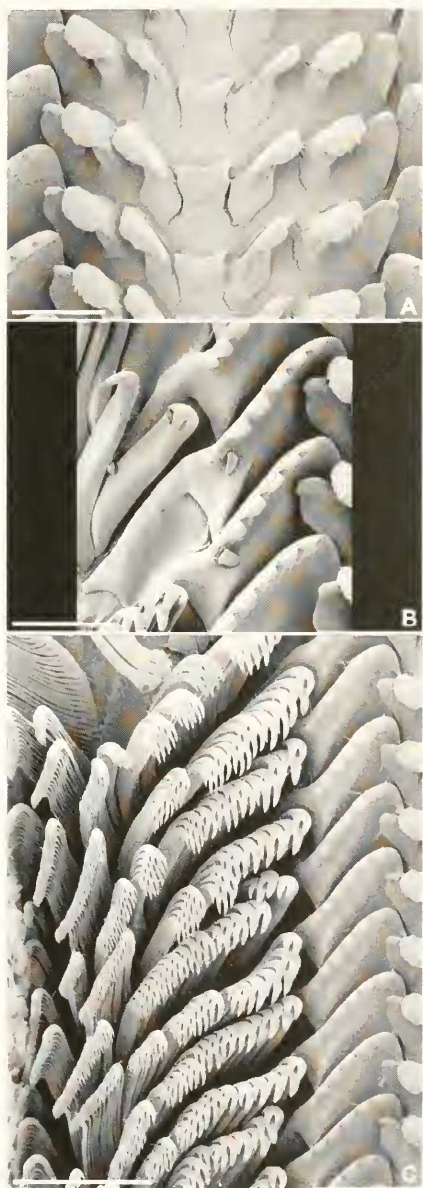


FIG. 45. Radula of *Helicina pitalensis*. A. Centrals. B. Comb-lateral. C. Marginals; scale bars 50 μ m (A, B), 100 μ m (C).

Juveniles are roundly angulated, and in some cases a few rows of periostracal hairs are present at the periphery.

Internal Shell Structures: (Fig. 41)

Teleoconch Surface Structure (Fig. 42): The transitional structure is developed, but as in *Helicina funcki* the pattern of oblique diverging grooves continues up to the aperture. In the shell illustrated, the grooves remain finer than in *H. funcki* (see 4th whorl), but this aspect is subject to individual variation.

Embryonic Shell (Fig. 43): The embryonic shell of *Helicina pitalensis* is very similar to that of *Helicina funcki*. The specimens measured came from altitudes of nearly 1,000 m. In comparison with the *H. funcki*-populations, the intermediate size therefore suggests equal dimensions, assuming a similar dependence on altitude.

Diameter: 1,089 μ m (\pm 23) (1,040–1,150) (n = 10) (IR 579, IR 1013, IR 1028, IR 1485).

Operculum (Fig. 44): Slightly calcified, calcareous plate leaving a free margin, thickened towards columellar side. Color dark reddish-brown to even black, only non-calcified margin transparent. Columellar side regularly S-shaped, upper end acute and pointed, lower end well rounded.

Animal (Fig. 337C): Only specimens that were very similarly colored from Bajo Bonito were studied. The foot is whitish-yellowish

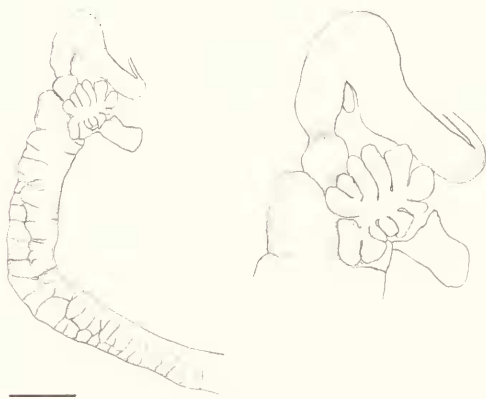


FIG. 46. Female reproductive system of *Helicina pitalensis*, apical complex enlarged, IR 579; scale bars 2 mm (left), 1 mm (right).

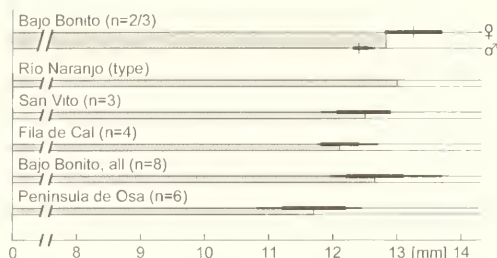


FIG. 47. Shell height of different populations of *Helicina pitaisensis* in Costa Rica, according to Table 5; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males or total"; upper line: females, lower line: males if separate; in between and shaded: average of both for comparison with populations of unknown sex.

throughout, the head region, especially around the black eyes and occasionally the upper part of the snout, is distinctly white. The tentacles become gradually darker towards their tips. The mantle has a whitish pigmentation.

Radula (Fig. 45): Only two specimens were investigated. The cusps on the A- and C-central are vestigial, only the B-central bears 5 to 9 cusps. Comb-lateral with 6–8 cusps, cusps on marginals slowly increasing in number. Radula with about 95–99 rows of teeth.

Female Reproductive System (Fig. 46): Only three female specimens were available for dissection. The pallial reproductive system closely resembles that of *Helicina funcki*.

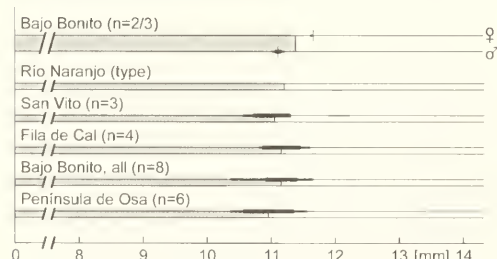


FIG. 48. Minor diameter of shell of different populations of *Helicina pitaisensis* in Costa Rica according to Table 5; for explanations see Fig. 47.

The bursa copulatrix differs in that it is as elongated as the whole organ, and the lobes project from a central axis and are much shorter, similar to those in the other species, although they are occasionally further subdivided. The provaginal sac seems to be smaller than in *Helicina funcki*.

Morphometry and Sexual Dimorphism

Despite the number of lots of *Helicina pitaisensis*, the material for morphometric analysis is scant because of a high proportion of juvenile shells.

Individuals from the lowlands of the Península de Osa differed from the typical specimens in having a more prominent aperture. The few individual records summarized as "Península de Osa" originate from the same region near Estación Sirena and were compared to populations from "San Vito", "Bajo Bonito" and "Fila de Cal", which are located close to each other in the mountainous country on the southern Pacific side (Fig. 52). The only specimens whose sex was determined belong to the population of Bajo Bonito. Any comparisons in this species can only hint at possible tendencies because of the scanty data.

Morphometry: The different populations show remarkably little differences in their minor diameter (Table 5, Fig. 48), which therefore provides a good reference for the pattern of differences among the populations for other measurements (Figs. 47, 49–51). The population "Península de Osa" displays the highest deviations; the shells are relatively less elevated in every respect (height, height of last whorl and columellar axis), but the aperture and outer lip is much more expanded. This confirms the observations noted above (Fig. 52). In general, the "Bajo Bonito" population best matches the type in proportions and size. This excludes a correlation of the differing shell shape of the "Península de Osa" specimens to the altitude, because the type lot also originates from lowlands (200 m) whereas the other sites are located at 700 to 1,160 m (San Vito). Thus, the special shell shape of the population "Península de Osa" seems to be a local peculiarity. Furthermore, current data do not support a correlation of shell size and altitude as for *Helicina funcki*.

TABLE 5. Measurements of different populations of *Helicina pitaleensis* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens; only population in last column separated in females and males, these individuals are also included in "Bajo Bonito, all" (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

"San Vito" (altitude 1160 m) lots IR 1016						"Fila de Cal" (altitude 600–780 m) lots IR 191, 209, INBio 1485456, INBio 3542525				
	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	12.48	0.47	11.78	12.89	3	12.12	0.30	11.75	12.72	4
Maj. diam.	12.34	0.37	11.78	12.65	3	12.31	0.19	11.96	12.58	4
Min. diam.	11.04	0.34	10.53	11.31	3	11.13	0.30	10.81	11.60	4
Outer lip	8.46	0.08	8.39	8.58	3	8.48	0.27	7.93	8.82	4
Last whorl	10.02	0.31	9.56	10.33	3	9.84	0.25	9.36	10.14	4
Col. axis	9.45	0.40	8.85	9.79	3	9.39	0.48	8.91	9.88	4

"Bajo Bonito, all" (altitude 920–980 m) lots IR 221, IR 579, IR 1028, IR 1485						"Península de Osa" (altitude 0–20 m) lots INBio 3542542, INBio 1482627, INBio 1482837, INBio 1482842, INBio 1485173				
	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	12.64	0.45	11.96	13.70	8	11.69	0.50	10.78	12.44	6
Maj. diam.	12.49	0.33	12.07	13.12	8	11.95	0.43	11.30	12.62	6
Min. diam.	11.13	0.27	10.33	11.66	8	10.93	0.40	10.35	11.54	6
Outer lip	8.51	0.27	7.85	9.08	8	8.78	0.42	8.25	9.25	6
Last whorl	10.21	0.29	9.68	10.78	8	9.77	0.39	9.27	10.30	6
Col. axis	9.50	0.33	8.75	10.48	8	8.89	0.52	7.91	9.67	6

"Bajo Bonito" (altitude 980 m) lots IR 579, IR 1028, IR 1485						
	Sex	Mean value	Deviation	Min	Max	Number
Height	f	13.26	0.44	12.82	13.70	2
Height	m	12.41	0.16	12.29	12.65	3
Maj. diam.	f	13.09	0.04	13.05	13.12	2
Maj. diam.	m	12.34	0.19	12.17	12.63	3
Min. diam.	f	11.64	0.02	11.62	11.66	2
Min. diam.	m	11.08	0.07	10.98	11.18	3
Outer lip	f	8.81	0.28	8.53	9.08	2
Outer lip	m	8.61	0.18	8.35	8.88	3
Last whorl	f	10.67	0.12	10.55	10.78	2
Last whorl	m	10.21	0.15	10.07	10.43	3
Col. axis	f	9.95	0.53	9.42	10.48	2
Col. axis	m	9.43	0.10	9.27	9.54	3
Weight	f	0.074	0.000	0.074	0.074	1
Weight	m	0.121	0.024	0.091	0.156	3
Volume	f	0.603	0.000	0.603	0.603	1
Volume	m	0.507	0.027	0.476	0.547	3

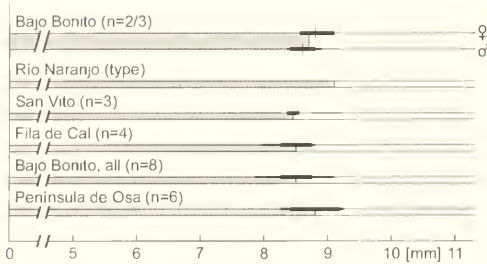


FIG. 49. Expansion of outer lip of different populations of *Helicina pitakensis* in Costa Rica according to Table 5; for explanations see Fig. 47.

Sexual Dimorphism: Although not well supported, the data for only two females and three males (Table 5, Figs. 47–51, upper row) suggest that females are bigger. The clear differences between both sexes for height, minor diameter, and height of last whorl may be only a coincidence.

Habitat

My live material came from two localities, near Bajo Bonito and near San Vito. They are characterized by steep mountain forests, probably primary rain forests, the first bordered by secondary growth and small manually tended agricultural areas. *Helicina pitakensis* lives in arboreal environments mainly on the underside of leaves of palms and Heliconiaceae. It was also found in the dried and curled-up leaves of abandoned banana trees. It thus has a very similar habitat as *H. funcki*.

Distribution (Fig. 53)

According to the relatively few records, *Helicina pitakensis* is confined to the southern

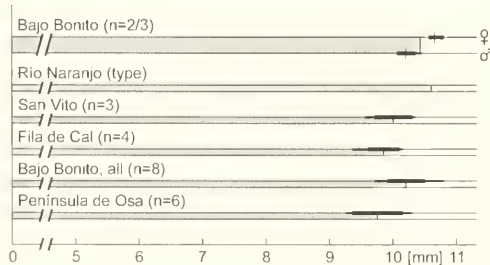


FIG. 50. Height of last whorl of different populations of *Helicina pitakensis* in Costa Rica according to Table 5; for explanations see Fig. 47.

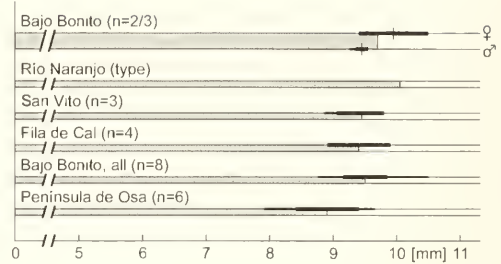


FIG. 51. Height of columellar axis of different populations of *Helicina pitakensis* in Costa Rica according to Table 5; for explanations see Fig. 47.

Pacific slopes and coastal lowlands in Costa Rica. On the Península de Osa and in the Fila de Cruces it is found at various localities. From the area around the type locality and the connecting area to the southern localities there are no recent records. This may be explained by lack of investigations in these areas and the relatively low abundance of the species on one hand, and the fact that the Pacific plains were transformed into agricultural plantations to a large extent starting in the 1950s.

The records of Pittier date back to the end of the 19th century when the areas were largely unexplored and under closed forest cover. Assuming that the interpretation of the records listed in von Martens (1900) is correct, *H. pitakensis* at least was well distributed over the area of the southern Pacific plain, replacing *H. funcki* in this region. In the Fila Cruces area and on Península de Osa, *H. pitakensis* is found sympatrically with *H. talamancensis*.

A typical specimen (ZMB 45501) of *H. pitakensis* is labeled as originating from La Paz, a location at the Río Sarapiquí north of the Cordillera Central on the Caribbean slope. This location seems to contradict the assumed distribution. Pending better knowledge, it is considered here to be erroneous.

Discussion

The species most resembles *Helicina funcki*, which is of about equal size and shows the same shell ornamentation. *Helicina pitakensis* is relatively higher and has more convex whorls. All specimens of *H. funcki* studied show neither banding nor the distinct angulation of the periphery. The strong denticle at the transition of the basal outer lip to the columella is characteristic for *H. pitakensis*, whereas it lacks the groove or angulation in the transition from the columella into the body whorl. Fur-



FIG. 52. Variations in Costa Rican *Helicina pitalensis*: shell height in figures reflects the mean value (enlarged), each shell originates from the respective locality.

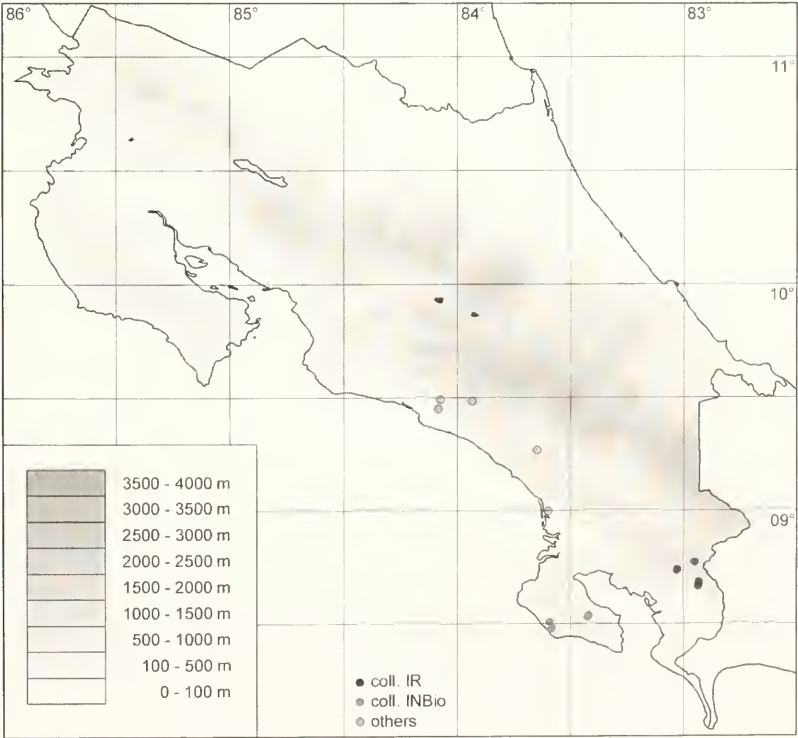


FIG. 53. Records of *Helicina pitalensis* in Costa Rica.

thermore, the soft body color differs and is constantly lighter in *H. pitalensis*.

The interpretation of the additional records of *H. funcki* listed in von Martens (1900) in SW-Costa Rica is difficult, because one of these locations became the type locality of *H. pitalensis* with description of this species by Wagner. Von Martens (1900) remarked: "some specimens banded and others more elevated", obviously for the specimens from El Pital. As here, Wagner saw only the holotype from the ZMB. If the remark of von Martens (1900) also referred to the specimens from the other locations, it would render their identification as *H. pitalensis* very likely. Although other material of Pittier is kept in the ZMB or the MHNN respectively, these lots could, unfortunately, not be found in either of the collections and thus could not be verified. According to personal information of Zaidett Barrientos (INBio), those parts of the historical collections in Costa Rica in the Museo Nacional in San José could not yet be found when she searched for this material. The museum had passed through several crises and the whereabouts of the material is uncertain. Regarding the fact that, according to the present data, *H. funcki* and *H. pitalensis* do not occur sympatrically and the latter species has not been recorded from the southern Pacific plain (except the one doubtful record from the Peninsula de Osa, see: under *H. funcki*) and the questionable interpretation of von Martens' remark, it seems more appropriate, until better knowledge comes along, to refer the records from "Bay of Terraba, Tocori in the valley of the Río Paquita, middle part of the Río Saveque and lower part of the Río Pacuare (Pittier)" also to *H. pitalensis*.

The record of *Helicina amoena* L. Pfeiffer, 1849, for Costa Rica by Monge-Nájera (1997) was based on the material in the INBio collection. The subsequent revision of the material revealed one lot of *H. amoena* (INBio 1485173) collected and determined before 1997, on the basis of which the publication must have been based. This specimen can clearly be referred to *H. pitalensis* in its typical form from the Peninsula de Osa. *Helicina amoena* is distinguished from *H. pitalensis* by its less elevated shell, which is more strongly angulated at the periphery and marked with distinct spiral striations. The color is also different. Except for one doubtful record from Panama by von Martens (1890) ("*Helicina amoena* var. b" from Cham-

pion) *H. amoena* has not yet been reported south of the Mosquito Coast of Nicaragua (Fluck, 1906: Mosquito Coast: NW Kukallaya, Wounta River; Jacobson, 1968: Bonanza). The original material of this doubtful record was assumed to be in the collection of the ZMB, as is other material of Champion, but it remains lost, although it was also searched for under other possible designations. It was later cited by Pilsbry (1910, 1926a), but who claimed not to have seen the specimen.

All recent records of *H. pitalensis* refer more to the south than the type locality. The specimens from the area of the Fila Cruces (Linda Vista, Fila Cal, San Vito) at higher altitudes (about 6001,000 m) are very similar to the type material. Only the basic lemon-yellow color is sometimes replaced by light orange-brownish. Specimens from the Peninsula de Osa sometimes lack the band and show certain deviations in shape and a stronger inflation of the whorls immediately below the suture. But because other characteristics do not differ (e.g., color, development of columellar region, protruding denticle at the transition of outer lip to columella, roundly angulated periphery) and adult material from other locations on the Peninsula de Osa is not available, a separation of this form is not yet warranted.

Helicina (Tristramia) tenuis
L. Pfeiffer, 1849

- Helicina tenuis* L. Pfeiffer, 1849: 124–125 (not figured)
Helicina vernalis Morelet, 1849: 20 (not figured)
Helicina tenuis – L. Pfeiffer, 1850: 40, pl. 7, figs. 33, 34
Helicina tenuis – L. Pfeiffer, 1852a: 372
Helicina vernalis – L. Pfeiffer, 1852a: 372
Helicina tenuis – L. Pfeiffer, 1852b: 269
Helicina vernalis – L. Pfeiffer, 1852b: 269–270
Helicina vernalis – L. Pfeiffer, 1853: 71, pl. 10, figs. 12–14
Helicina chiapensis L. Pfeiffer, 1856: 237 (not figured); 1857: 380 (not figured)
 ?*Helicina lindeni* – Tristram, 1862: 5: Guatemala: neighbourhood of Dueñas [according to Tristram, 1864] (Salvin) [non L. Pfeiffer, 1849]
 ?*Helicina lindeni* – Sowerby, 1866: 288, pl. 272, figs. 258260 [non L. Pfeiffer, 1849]
Helicina chiapensis – Sowerby, 1866: 288, pl. 272, figs. 255–257

- Helicina vernalis* – Sowerby, 1866: 288, pl. 273, fig. 273
- Helicina tenuis* – Bland, 1866: 9
- Helicina vernalis* – Bland, 1866: 9
- Helicina chiapensis* – Bland, 1866: 9
- Helicina vernalis* – Reeve, 1874: pl. 18, fig. 156
- Helicina chiappensis* [sic] – Reeve, 1874: pl. 13, fig. 110
- Helicina vernalis* – von Martens, 1875: 649: Guatemala: Coban, Vera Paz
- Helicina vernalis* – von Martens, 1876: 259: Guatemala: Coban
- Helicina lindeni* – Angas, 1879: 484: Costa Rica [non L. Pfeiffer, 1849]
- ?*Helicina lindeni* var. *minor* – Ancey, 1886: 258–259: Honduras, Atlantic coast (smaller specimens)
- Helicina tenuis* – von Martens, 1890: 34–35: Central Mexico: Sayula in Jalisco, Irapuato near Guantajuoto; E-Mexico: Soledad, between Cordova and Orizaba; SE-Mexico: Chiapas; Teapa and San Juan Bautista in Tabasco, Tapinapa; Yucatan; N-Guatemala: Peten Province; Cubilguitz, valley of the River de la Pasión; Coban; San Gerónimo and the neighbouring mountains in Vera Paz; Panzos; Chacoj; San Juan (all in the valley of the Polochic River); Purula; S-Guatemala: Totonicapam mountains 8,500 to 10,500 feet (small variety); El Reposo 800 feet; Las Mercedes 3,000 feet; Cerro Zunil 4,000 feet; San Isidro 1,600 feet, all on Pacific slope; Zapote, on the slope of the Volcan de Fuego; Nicaragua: Toro Rapids?; Costa Rica
- Helicina tenuis* var. *chiapensis* – Pilsbry, 1892: 339: Mexico: Tabasco: Poana (Rovirosa)
- Helicina (Oligyra) lindeni* – Fischer & Crosse, 1893: 416–420, pl. LVI, figs. 1–3: same data as von Martens (1890) [non L. Pfeiffer, 1849]
- Helicina tenuis* – Biolley, 1897: 5: Costa Rica: Turrubares, 200 m [San Pablo de Turrubares, about 09°55'N, 84°27'W, San José Province] and La Paz, 900 m, en el camino del Sarapiquí [along the River Sarapiquí] [not exactly localized, near Isla Bonita?, about 10°15'30"N, 84°11'W, Alajuela Province]
- Helicina tenuis* – von Martens, 1900: 604: SE-Mexico: Poana, Tabasco; Honduras: East Coast – smaller spec.; NE-Costa Rica: La Paz, on the road to the Río Sarapiquí Sarapiquí [not localized, near Isla Bonita?, about 10°15'30"N, 84°11'W, Alajuela Province] (Biolley); Central Costa Rica: Alajuela, 900–1,000 m [town or province?, town about 10°01'30"N, 84°13'W] (Orosco), SW-Costa Rica: Turrubares, 200 m [San Pablo de Turrubares, about 09°55'N, 84°27'W, San José Province] (Biolley); along the Río de los Platanales and the Golfo Dulce [correct: Río de los Platanares, S of Puerto Jiménez, Peninsula de Osa, about 08°31'30"N, 83°18'W, Puntarenas Province] (Pittier)
- Helicina vernalis* – Wagner, 1905: 233–234, pl. XIII, fig. 13a–c: Guatemala: Petén; Verapaz: Río Polochic
- Helicina vernalis verapazensis* Wagner, 1905: 234, pl. XIII, fig. 14: Guatemala: Verapaz
- Helicina tenuis pittieri* Wagner, 1910a: 303–304, pl. 60, fig. 24
- Helicina tenuis* – Wagner, 1910a: 302–303, pl. 60, figs. 15–23, 25: S-Mexico to Panama: Mexico: Tabasco and Chiapas; Guatemala: Coban, Totonicapam, St. Isidoro, Río Polochic, Mercedes and Vera Paz; Costa Rica: Turrubares [San Pablo de Turrubares, about 09°55'N, 84°27'W, San José Province] and Alajuela [town or province?, town about 10°01'30"N, 84°13'W]
- Helicina tenuis* var. *lindeni* – Hinkley, 1920: 49, 52: Guatemala: Jocolo plantation on north side of Lake Isabal; Alta Verapaz: Chama between Río Tsalbha and Río Negro [non L. Pfeiffer, 1849]
- Helicina (Tristramia) tenuis* – Baker, 1922a: 50, pl. III fig. 7, pl. IV, fig. 14 (radula)
- Helicina (Tenuis) tenuis* – Baker, 1922b: 35–36: Mexico: S Vera Cruz, near Hacienda de Cuatolapam (Río San Juan – Arroyo Hueyapam, canton of Acayacan (Michigan-Walker-Expedition)
- Helicina tenuis* – Pilsbry, 1926a: 59, 71: Panama: Los Santos Province: Tonosi (Olsson)
- ?*Helicina tenuis* var. – Pilsbry, 1930: 339: Panama: Barro Colorado Island (Pinchot-Expedition)
- Helicina (Tristramia) lindeni* – Bequaert & Clench, 1933: 543: not found again in Yucatán [non L. Pfeiffer, 1849]
- Helicina tenuis* – Goodrich & van der Schalie, 1937: 12, 15, 32: Guatemala: Petén: region of headwater of Río San Pedro de Mártir, lower Río de la Pasión; Alta Verapaz: upper part of Río de la Pasión
- Helicina tenuis* – van der Schalie, 1940: 6, 9, 10: Guatemala: Alta Verapaz: Pacala and Chama, 290 m a.s.l., Samac, 1,300 m a.s.l. [W of Coban], Panzamal, 1,250 m a.s.l. [S of Lanquín] (Stuart)

Helicina (Helicina) tenuis – Haas, 1949: 137–138: Guatemala: Chimaltenango: Yepocapa, 4800 ft.; Zacapa: Santa Clara, valley in the interior of the Sierra de las Minas, N of Cabañas, 5500 ft. (Wenzel & Mitchell)

Helicina tenuis – Bequaert, 1957: 207: Chiapas: Selva Lacandona: Monte Libano, 600 m, El Real, 600 m

Helicina tenuis tenuis – Thompson, 1967: 228–229: Mexico: Campeche: 10.2 mi E Escárcega, rare (1 spec., dead), Chiapas: 15.8 mi NW Ocozocoautla

Helicina tennuis [sic] – Pérez & Lopez, 1993: 27: Nicaragua

Helicina oweniana – Monge-Nájera, 1997: 113: Costa Rica [in part] [non L. Pfeiffer, 1849]

Synonymy

Helicina vernalis Morelet, 1849

Helicina chiapensis L. Pfeiffer, 1856

Helicina vernalis verapazensis Wagner, 1905

Helicina tenuis pittieri Wagner, 1910

Original Description

“Hel. testa, turbinata, tenuissima, vix striatula, pellucida, corneo-albida, rubro obsolete trifasciata; spira conica, acuta; anfractibus 6 vix convexiusculis, ultimo basi planiusculo; apertura fere verticali, triangulari-semiovali; columella brevi, basi retrorsum subdentata, superne in callum nitidum, circumscriptum, dilatata; peristomate tenui, angulatim expanso, margine basali cum columellae basi angulum formante.

Diam. 11, altit. $8\frac{1}{2}$ mill.

From Yucatan.”

Type Material

BMNH 20010496.1–7 “Yucatan & Barbadoes, coll. Hugh Cumming”

The type lot contains seven specimens, labeled as originating from Yucatan and Barbadoes. The latter locality is not given in the original description. In fact, the lot is a mixture of two species, and only five specimens agree with the description of *Helicina tenuis*. The other two exhibit a less elevated spire, less convex whorls and the first whorls increase more rapidly in size. Furthermore, the shells, lacking the spiral color bands, are colored uniformly whitish, except for a broken nearly transparent thin spiral line above the periphery. Finally, the characteristic denticle of *H. tenuis* at the basal outer lip is less strongly developed. Thus, these specimens (BMNH 20010496.6–7) are excluded from the syntype lot of *Helicina tenuis*, because they do not agree with the original description and the later given figure. It is very likely that the lot was mixed subsequently to the studies of L. Pfeiffer.

The largest specimen is **here selected as lectotype** (Fig. 54), because it best agrees with the figure in L. Pfeiffer (1850). It is the only specimen in the lot with banding, without operculum and about the size given in the description. In comparison with the figure the bands are faded, but it may be an exaggeration in the drawing since they are described as “rubro obsolete trifasciata”.

Dimensions:

Lectotype BMNH 20010496.1:

9.8/9.8/10.8/8.9/6.5/7.7/7.6 mm

Paralectotypes BMNH 20010496.2–5:

9.6/9.1/10.4/8.4/6.4/7.5/7.2 mm



FIG. 54. *Helicina tenuis*, lectotype, BMNH 20010496.1, height 9.8 mm; scale bar 2.5 mm.

8.9/8.7/9.4/8.1/5.6/6.8/7.0 mm
 9.8/9.0/10.0/8.3/6.0/7.2/7.5 mm
 8.7/7.9/8.7/7.3/5.4/6.4/6.7 mm

It is remarkable that even the type lot shows a comparatively great variation in size and shape (e.g., lectotype and smallest paralectotype).

Type Locality

"Yucatán" [Not clear, whether it refers to the Mexican State of Yucatán or to the whole Yucatán Peninsula, shared by Mexico, Guatemala, and Belize. The present data of distribution suggest its origin rather in the Mexican State of Campeche or the Guatemalan Petén Department.]

Type Material of Synonymous Taxa or Similar Species

Helicina vernalis Morelet, 1849

Type Material: BMNH 1893.2.4.1991–1993: Morelet coll., purchased from H. Fulton. The Morelet collection was bought by H. Fulton and later purchased by the BMNH. Fischer & Crosse (1893) studied the original material in the Morelet collection and figured a shell that can be identified by the mark of a "x" and the clear similarity to the figure. This shell is **here selected as lectotype** of *Helicina vernalis* (BMNH 1893.2.4.1991) (Fig. 55), because it is uncertain whether Fischer & Crosse's comment in the figure caption (pl. LVI, fig. 1, 1a, 1b: "premier type de l' *Helicina vernalis*") can be regarded as a type selection. The lectotype is colored uniformly whitish and

still possesses its operculum, whereas the paralectotypes are whitish below the periphery and above tinged reddish-brownish or yellowish with two reddish-brownish bands respectively.

Dimensions:

Lectotype BMNH 1893.2.4.1991:

9.9/9.9/10.8/8.9/6.5/7.7/7.5 mm

Paralectotypes BMNH 1893.2.4.1992–1993:

9.4/9.4/10.3/8.3/6.3/7.5/7.2 mm

9.2/9.2/10.0/8.2/6.2/7.3/7.0 mm

Type Locality: "Petenensis sylvas" [Guatemala, Petén Department]

Helicina chiapensis L. Pfeiffer, 1856

Type Material: Syntype ZMB 65624: leg. Ghiesbreght, ex coll. L. Pfeiffer (Fig. 56)

The description of *Helicina chiapensis* was published in two journals. In the earlier publication (December 1856), L. Pfeiffer stated that he had received specimens from Hugh Cuming, leg. Ghiesbreght, which he probably kept in his collection. The second publication (May 1857) refers to material in the collection Hugh Cuming, leg. Ghiesbreght. Thus additional syntypes are possibly in the collection of the BMNH housing the main collection of Hugh Cuming, although they have not yet been found in the type collection.

Dimensions (height/greatest diameter/minor diameter):

Syntype: 10.2/11.4/9.4 mm

Type Locality: "Mexico, Chiapa" [Mexico, State of Chiapas]



FIG. 55. *Helicina vernalis*, lectotype, BMNH 1893.2.4.1991, height 9.9 mm; scale bar 2.5 mm.

Helicina lindeni L. Pfeiffer, 1849

Helicina lindeni L. Pfeiffer, 1849: 123 (not figured)

Helicina lindeni – L. Pfeiffer, 1850: 52, pl. 8, figs. 25, 26

Material Studied: *Helicina lindeni* var. – BMNH 20010757: Mexico, Hugh Cuming coll., three specimens

The type material could not be located in the collection of the BMNH, although it was listed in the catalogue of the BMNH collection by L. Pfeiffer (1852b: 282) as coming from the type locality Tapinapa, Mexico (leg. Linden).

The specimens in BMNH 20020757 definitely do not belong to *Helicina tenuis*, but rather agree well with the original description of *Helicina lindeni*, especially, because in contrast to *H. tenuis* it is slightly angulated at the periphery and less elevated. None of the shells shows a trace of spiral color bands. The outer lip is more reflexed.

Helicina tenuis pittieri Wagner, 1910

Type Material: Holotype ZMB 103241: leg. Pittier

Because the original description refers to one specimen in the ZMB which also matches the figure it is the holotype (Fig. 57).

Dimensions:

Holotype: 9.2/8.6/9.4/8.0/6.0/7.4/7.1 mm

Type Locality: "Costa Rica, Río de los Plutunales, Golfo Dolce" [correct: Río de los Platanares, S of Puerto Jiménez, Península de Osa, about 08°31'30"N, 83°18'W, Puntarenas Province]

Examined Material

LEG. I. RICHLING

Guanacaste: 3 km E Nuevo Arenal, 10°31'53"N, 84°52'50"W, 640 m a.s.l.: property of pension Villa Decary, rain forest: 03.03.1997: (IR 52); 01.03.1999: (IR 715); 02.03.1999: (IR 722); 31.07.1999: (IR 880); 23.02.2000: (IR 1266); along small creek E of Villa Decary: 04.03.1999: (IR 730)

Heredia: S Puerto Viejo de Sarapiquí, Zona Protectora La Selva, near OTS-Station, about 10°25'53"N, 84°00'18"W, 60 m a.s.l., 05.09.1999: (IR 1057); (IR 1058); 12.02.2000: (IR 1181)

Puntarenas: Reserva Natural Absoluta Cabo Blanco, 09°35'16"N, 85°05'45"W, 30 m a.s.l.: Sendero Danes and trail from entrance: 25.08.1999: (IR 1001); (IR 1002); 27.02.2000: (IR 1289); (IR 1291); Sendero Sueco: 02.03.2001: (IR 1481)

INBIO COLLECTION

Guanacaste: 500 m E de la Estación Almendros, 11°02'04"N, 85°31'10"W, 280 m a.s.l., leg. Elba Lopez, 01.08.1994: 1 ad. (INBio 1477167)

Parque Nacional Barra Honda, Los Mesones: 10°10'12"N, 85°21'03"W, 300 m a.s.l., 29.05.1993: 2 ads. (INBio 1463476); 10°10'12"N, 85°20'50"W, 100 m a.s.l., 31.05.1993: 4 ads., 1 s.ad. (INBio 1463452) (all leg. malacological staff of INBio)

Refugio Nacional de Vida Silvestre Bosque Diría, Sector Diría: Sendero Espavel, 10°10'19"N, 85°35'44"W, 220 m a.s.l.: leg. Alexander Alvarado Mendez, 13.05.1999: 6 ads., 4 juvs. (INBio 3096450); 200 m a.s.l.: leg. A. Berrocal, 22.11.1998: 2 ads. (INBio



FIG. 56. *Helicina chiapensis*, syntype, ZMB 65624, height 10.2 mm; scale bar 2.5 mm.

3435759); *Camino a Esperanza*, 10°10'32"N, 85°35'11"W, 260 m a.s.l.: 14.05.1999: 1 ad., 1 s.ad., 2 juvs. (INBio 1498286); 2 ads. (INBio 1498287) (all leg Alexander Alvarado Mendez)

Puntarenas: *Parque Nacional Carara: Quebrada Bonita*, 09°46'29"N, 84°36'34"W: 50 m a.s.l., 03.06.2000: 4 s.ads. (INBio 3324332); 100 m a.s.l., 02.07.2000: 3 ads. (INBio 3129469); *Carara, sendero Laguna Meandrica*, 09°48'20"N, 84°35'02"W, 100 m a.s.l.: 15.07.2000: 1 s.ad. (INBio 3395010) (all leg. malacological staff of INBio)

Parque Nacional Corcovado: Río Sirena, 08°30'25"N, 83°29'23"W, 545 m a.s.l.: leg. Enia Navarro, 24.05.1995: 1 ad. (INBio 1484663); 2 km SW del Mirador, 08°32'30"N, 83°30'57"W, 200 m a.s.l.: leg. Socorro Avila, 22.05.1997: 1 ad. (INBio 1487810)

Reserva Forestal Golfo Dulce: Fila Casa Loma, 1,600 m S de la Escuela de Rincón, 08°41'33"N, 83°29'17"W, 170 m a.s.l.: leg. Socorro Avila, 10.10.1996: 2 ads. (INBio 1487328); *Península de Osa, Instalaciones de IDA*, 08°41'38"N, 83°29'07"W, 60 m a.s.l.: leg. Ramon Angulo, 07.06.1994: 1 ad. (INBio 1480502)

Reserva Natural Absoluta Cabo Blanco: Sector Balsitas, Sendero Central, 09°35'02"N, 85°07'26"W, 120 m a.s.l.: 18.05.1994: 6 juv. (INBio 1473990); 2 ads. (INBio 1475801); 1 ad. (INBio 1475805) (all leg. Zaidett Barrientos); *Sector Cabuya, Sendero Sueco, Río Ariolo*, 09°35'16"N, 85°05'41"W, 20 m a.s.l.: leg. Ulises Chavarría, 08.11.1994: 1 ad. (INBio 1480012); *Sector San Miguel, Sendero Maven*, 09°35'09"N, 85°08'12"W, 200 m a.s.l.: leg. Zaidett Barrientos, 17.05.1994: 1 ad. (INBio 1474149)

Cóbano, Estación Cabo Blanco, 09°35'30"N, 85°05'45"W, 15 m a.s.l., leg. malacological staff of INBio, 09.01.1993: 4 ads., 5 s.ads., 3 juvs. (INBio 1465481)

Sendero Camino Maven, orilla de quebrada San Miguel, 09°35'18"N, 85°08'12"W, 100 m a.s.l., leg. Alexander Alvarado Mendez, 21.01.1999: 2 ads. (INBio 1498272); 2 ads. (INBio 1498276)

Quebrada San Miguel, 09°35'15"N, 85°08'15"W, 100 m a.s.l., leg. Socorro Avila, 05.10.1995: 1 ad. (INBio 1484853)

Alajuela: San Ramón, 10°05'19"N, 84°29'18"W, 1,060 m a.s.l., leg. malacological staff of INBio, 16.09.1993: 1 ad. (INBio 1464319)

Estación Playuelas, 50 m del Río Frio, 10°57'29"N, 84°44'55"W, 40 m a.s.l., leg. Kattia Martínez, 08.01.1994: 1 ad. (INBio 1479297)

OTHER SOURCES

COSTA RICA

Guanacaste: Las Cascadas, Quebrada San Diego, 10°10'59.5"N, 85°20'18.5"W, leg. D.G. Robinson & J.M. Montoya, 20.09.1998 (APHIS PPQ USDA)

Karst exposure, Cerro Barra Honda, approx. 10°10'10"N, 85°22'10"W, leg. D.G. Robinson & J.M. Montoya, 19.09.1998 (APHIS PPQ USDA)

Nicoya [about 10°08'30"N, 85°27'30"W], leg. H.G. Lee, ex G.D. Robinson, W.F. Webb: 1 ad. (UF 166944)

Federal de Nicoya [about 10°08'N, 85°26'W], leg. Univ. Alabama, M. Smith coll. (MS-15277): 12 ads. (UF 95336)

2.2 mi SE Nicoya [about 10°07'30"N, 85°26'W], 500 ft., leg. F.G. Thompson (FGT-106), 10.08.1964: 1 ad. (UF 214333)



FIG. 57. *Helicina tenuis pittieri*, holotype, ZMB 103241, height 9.2 mm; scale bar 2.5 mm.

- 3.8 mi S Nicoya [about 10°05'N, 85°28'W], leg. F.G. Thompson (FGT-111), 11.08.1964: 1 ad. (UF 35511)
- 1.2 mi E Caimital [about 10°04'N, 85°27'W], leg. F.G. Thompson (FGT-109), 11.08.1964: 1 ad. (UF 214332)
- Monte Alto conservation area, near Pilangosta, Canton Hojancha, 10°00'48.1"N, 85°24'08.1"W, leg. D.G. Robinson & J.M. Montoya, 19.09.1998 (APHIS PPQ USDA)
- Alajuela: "Alajuela" [city or province?, town about 10°01'30"N, 84°13'W], Orosco (ZMB 103247)
- La Paz (Chem. du Sarapiquí) [not exactly localized, near Isla Bonita?, about 10°15'30"N, 84°11'W], leg. P. Biolley (#90): 2 ads. (MHNN)
- "San José Prov.:" San José [really San José, capital of Costa Rica?, or province later added and originally referring to San José in Alajuela Province, here preferred: 14 km NW of Upala, about 10°58'N, 85°08'W, Alajuela Province], leg. McGinty coll., ex Preston & Tomlin: 1 ad. (UF 160158)
- San José: Turubares, Versant du Pacifique [San Pablo de Turrubares, about 09°55'N, 84°27'W], 500 m a.s.l., leg. P. Biolley (#140), 06.1893: 21 ads., 1 s.ad. (MHNN)
- Cartago: Turrialba [about 09°54'30"N, 83°41'W], coll. C. Bosch, ex coll. Rolle, ex Wagner: 4 ads. (SMF 180786/4); coll. Rolle: 12 ads. (ZMB 103802)
- Puntarenas: Golfito [about 08°39'N, 83°10'W], leg. F.G. Thompson et al., 14.06.1964: 1 ad. (UF 35510)
- Costa Rica, without locality further specified: leg. McGinty coll.: 1 ad. (UF 263576); 1 ad. (UF 214331)
- GUATEMALA**
- El Petén: S of Sayaxche, beyond L Petexbatun, leg. J. Polisar, 31.08.1994: 4 ads. (UF 234127)
- Huehuetenango: Cave below Finca Chiblac, ca. 5 km W of San Ramon, 15°52'45"N, 91°14'34"W, 700 m a.s.l., leg. F.G. Thompson et al. (FGT-4828), 05.03.1991: 5 ads. (UF 190327); (UF 190329: 1 of 6 spec.)
- Alta Verapaz: 2 km WNW of Lanquin, 15°34'38"N, 89°59'19"W, 300 m a.s.l., leg. S.P. Christman (FGT-4791), 21.02.1991: 2 ads. (UF 190068)
- 4 km W of Lanquin, 15°34'37"N, 90°01'06"W, 330 m a.s.l., leg. F.G. Thompson (FGT-4793), 21.02.1991 (UF 190093: 1 of 5 spec.)
- 9 km W of Lanquin, 15°35'03"N, 90°03'20"W, 690 m a.s.l., leg. F.G. Thompson et al. (FGT-4787), 20.02.1991: 1 ad. (UF 190036); (UF 190045: 2 of 4 spec.)
- 11 km W of Lanquin, 15°33'29"N, 90°04'02"W, 1,000 m a.s.l., leg. F.G. Thompson et al. (FGT-4801), 22.02.1991: 2 ads. (UF 190142)
- 6.5 km SE of Lanquin, 15°32'52"N, 89°57'22"W, 400 m a.s.l., leg. F.G. Thompson (FGT-4796), 21.02.1991: 2 ads. (UF 190108)
- 8 km SE of Lanquin, 15°32'43"N, 89°56'49"W, 350 m a.s.l., leg. F.G. Thompson et al. (FGT-4797), 21.02.1991: 1 ad. (UF 190116)
- 2 km ESE Cojaj, 15°33'25"N, 90°06'56"W, 1,250 m a.s.l., leg. F.G. Thompson (FGT-4783), 20.02.1991: 3 ads. (UF 190006)
- 8 km by road N of Coban, 15°31'30"N, 90°23'11"W, 1,340 m a.s.l., leg. F.G. Thompson et al. (FGT-4776), 18.02.1991: 3 ads. (UF 189950)
- 4 km E of Coban, 1,260 m a.s.l., leg. F.G. Thompson et al. (FGT-4803), 23.02.1991 (UF 190156: 1 of 2 spec.)
- Coban, Sumichrast: 2 ads. (UF 214336); leg. Univ. Alabama, T.H. Aldrich coll. (THA-8198), ex Mohr coll.: 2 ads. (UF 095334)
- Limestone knoll 11 km S of Coban, 15°24'57"N, 90°24'09"W, 1,350 m a.s.l., leg. F. G. Thompson et al. (FGT-4805), 04.02.1991: 1 ad. (UF 190163)
- 2.5 km by road NE of Puente Chixoy, 15°21'32"N, 90°39'10"W, 810 m a.s.l., leg. F.G. Thompson (FGT-4781), 19.02.1991 (UF 189988)
- Limestone knoll 17.5 km NW of Tactic, 15°21'29"N, 90°25'25"W, 1,330 m a.s.l., leg. F.G. Thompson et al. (FGT-4764), 16.02.1991: 3 ads. (UF 189840)
- 10.5 km SE of El Tactic, 15°16'59"N, 90°18'11"W, 1,460 m a.s.l., leg. S.P. Christman (FGT-4810), 26.02.1991: 2 ads. (UF 190204)
- E of Finca el Volcan, leg. J. Schuster, 22.07.1984: 1 ad. (UF 114090)
- Izabal: Río Tameja, 12.9 km SSW Livingston, leg. F.G. Thompson (FGT-54), 04.07.1964: 1 ad. (UF 214330)
- Zacapa: La Union, Cerro Mona (N), 1,350-1,500 m a.s.l., leg. E.N. Smith, 20.06.1994: 1 ad. (UF 244447)
- Retalhuleu: Retalhuleu, leg. Univ. Alabama, T. H. Aldrich coll. (THA-8197) ex Mohr coll.: 2 ads. (UF 95335)
- Guatemala, without locality further specified: La Paz [localization?: perhaps Verapaz or in Honduras?], ex coll. S. G. A. Jaekel: 3 ads.

(HNC 39843); leg. Beal-Maltbie coll., ex W. Webb coll.: 1 ad. (UF 237376); leg. Beal-Maltbie coll., ex W. Webb coll.: 1 ad. (UF 237377)

EL SALVADOR

Ahuachapán: 6 km W of Atiquizaya, on road to Ahuachapán, leg. A. Zilch, 21.09.1951: 4 ads. (SMF)

HONDURAS

Colón: Limestone ridge, 2.6 km SW of La Brea, 15°45'39"N, 86°00'08"W, 100 m a.s.l., leg. F.G. Thompson (FGT-5253), 22.10.1993: 1 ad. (UF 212023)

Olancho: Vicinity of Magua Cave, ca. 15 km SSW of Gualaco, 14°56.5'N, 86°07.5'W, 940 m a.s.l., leg. F.G. Thompson et al. (FGT-5216), 11.03.1993: 4 ads. (UF 194339)

MEXICO

Guerrero: 1 km E Petaquillas, 1158 m a.s.l., leg. F.G. Thompson (FGT-1584), 03.11.1970: 9 ads. (UF 217551)

2.2 mi NNE of Mazatlan, 4800 ft., leg. F.G. Thompson (FGT-672), 14.06.1966: 1 ad. (UF 77607)

Limestone hill, 1 km NW of Naranjito, 18°05'03"N, 101°50'45"W, 675 m a.s.l., leg. F.G. Thompson (FGT-5087), 04.11.1992: 1 ad. (UF 200647)

Oaxaca: Lagunas, 259 m a.s.l., leg. F.G. Thompson, 18.07.1966: 2 ads. (UF 214337)

Limestone ridge, 4 km W of Cuauht, moc, 17°05'56"N, 94°54'25"W, 100 m a.s.l., leg. F. G. Thompson et al. (FGT-5271), 02.08.1993: 1 s.ad. (UF 211326)

Limestone knoll, 13 km ENE of Sarabia, 17°05'54"N, 94°56'34"W, 125 m a.s.l., leg. F. G. Thompson et al. (FGT-5269), 02.08.1993: 3 ads. (UF 211316); leg. F. G. Thompson (FGT-5280), 03.08.1993: 2 ads. (UF 211427)

Veracruz: 5 km ENE of Cuauht, moc, Oaxaca, 17°06'59"N, 94°51'10"W, 75 m a.s.l., leg. F.G. Thompson et al. (FGT-5273), 03.08.1993: 1 ad. (UF 211337)

7 km S, 7 km E of Catamaco, 350 m a.s.l., leg. F.G. Thompson et al. (FGT-4608), 03.01.1990: 4 ads. (UF 159375)

Laguna Encontada, 20.08.1962: 1 ad. (UF 214338)

Limestone knoll, 2 km SW of Plan Arroyo, 17°14'15"N, 94°37'36"W, 100 m a.s.l., leg. F.G. Thompson et al. (FGT-5278), 03.08.1993: 2 ads. (UF 211398)

Tabasco: 3 km N of Vicente Guerrero, 17°31'09"N, 92°56'00"W, 160 m a.s.l., leg. F.G. Thompson (FGT-4873), 03.04.1991: 3 ads. (UF 190725)

6.8 km W Teapa, leg. F.G. Thompson (FGT-427), 08.07.1965: 2 ads. (UF 214344)

Campeche: 16.4 km E Escárcega, leg. F.G. Thompson (FGT-406), 19.06.1965: 1 ad. (UF 19296)

Chiapas: 15.1 km W San Cristobal, 2469 m a.s.l., leg. F.G. Thompson (FGT-446), 15.07.1965: 1 juv. (UF 214335); 1 ad. (UF 214340)

18.3 km N Tuxtla Gutierrez, 1372 m a.s.l., leg. F.G. Thompson (FGT-465), 22.07.1965: 1 juv. (UF 214341)

12.9 km N Tuxtla Gutierrez, 1158 m a.s.l., leg. F.G. Thompson (FGT-459), 19.07.1965: 3 ads. (UF 214343)

4.8 km SSE Tuxtla Gutierrez, 823 m a.s.l., leg. F.G. Thompson (FGT-763), 25.07.1966: 2 ads. (UF 214345)

7.5 km NNE Huixtla, 183 m a.s.l., leg. F.G. Thompson (FGT-757), 23.07.1966: 1 ad. (UF 214346)

21.3 mi NW Huixtla, 300 ft., leg. D.R. Paulson et al., 31.07.1965: 2 ads. (UF 214339)

Stream, 44.4 km NW Ocozocoautla, 610 m a.s.l., leg. F.G. Thompson (FGT-464), 21.07.1965: 1 ad. (UF 214342)

25.4 km NW Ocozocoautla, 823 m a.s.l., leg. F.G. Thompson (FGT-462): 20.07.1965: 1 ad. (UF 19295)

34.1 km E, 16.4 km S Comitán, 1524 m a.s.l., leg. F.G. Thompson (FGT-441), 14.07.1965: 1 ad. (UF 214145)

Ruins of Palenque, leg. H.W. Campbell, 04.05.1970: 3 ads. (UF 214334)

Mexico, without locality further specified: leg. Univ. Alabama, T.H. Aldrich coll. (THA-8195): 2 ads. (UF 95291)

Description

Shell (Figs. 58, 335F–I): Conical-globose, semi-fragile to thin, sometimes semitransparent, medium sized and only slightly shiny to dull. Color: basic color yellowish to whitish-opaque to horn-colored, with up to three indistinct reddish bands on body whorl: one between suture and periphery and one or two below the periphery. The lower band only very weakly developed or obsolete. Surface textured with fine irregular growth lines and oblique grooves of different indi-

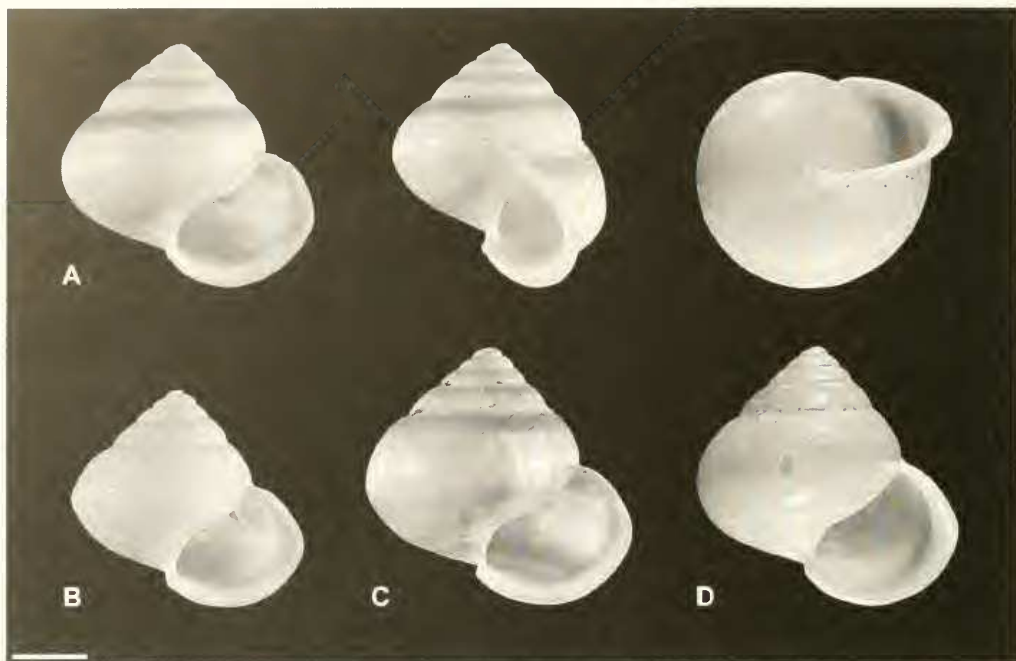


FIG. 58. *Helicina tenuis*. A–C. Cabo Blanco, IR 1001. A. Height 8.3 mm. B. Height 7.3 mm. C. Height 8.5 mm. D. La Selva, IR 1057, height 8.7 mm; scale bar 2.5 mm.

vidual orientation but of the same general direction (Fig. 60), causing the dull appearance. Embryonic shell with about 1 whorl, $4\frac{1}{4}$ –5 (lectotype: $4\frac{3}{4}$) subsequent whorls well inflated, remarkably convex, the last whorl regularly rounded or sometimes with a slight angulation at the periphery, under the suture slightly shouldered; whorls equally extending in size, forming a very regular conical, pointed spire. Suture deeply impressed. Aperture oblique and nearly straight, last whorl regularly descending and inserting exactly at the periphery. Outer lip always yellowish-white, slightly thickened and broadly expanded. Reflection nearly rectangular to the whorl; transition to columella with a remarkably protruding denticle. Columella short. Basal callus weakly developed and nearly completely smooth or very little granulated, umbilical area without groove.

Internal Shell Structures: (Fig. 59)

Teleoconch Surface Structure (Fig. 60): The transitional structure extends about half a

whorl, the subsequent pattern of oblique diverging grooves continues up to the aperture.

Embryonic Shell (Fig. 61): The structure resembles that of *Helicina funcki*, occasionally the pits are somewhat smaller. The embryonic shell size of the Costa Rican specimens agrees fairly well with the larger shells (see "Morphometry") of the type lot of *H. tenuis* which came from the Península de Yucatán. Diameter: $838\ \mu\text{m}$ (± 28) (780–900) ($n = 25$) (IR 1001, IR 1002); $834\ \mu\text{m}$ (± 27) (800–860)

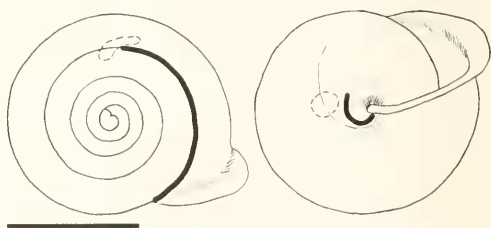


FIG. 59. Axial cleft and muscle attachments of *Helicina tenuis*, IR 1001; scale bar 5 mm.



FIG. 60. Teleoconch surface structure of *Helicina tenuis* on 2nd whorl; scale bar 100 µm.



FIG. 61. Embryonic shell of *Helicina tenuis*; scale bar 100 µm.

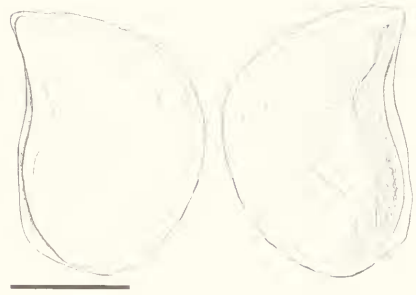


FIG. 62. Operculum of *Helicina tenuis*, IR 1001; scale bar 2 mm.

($n = 5$) (BMNH 20010496.1–5, type lot, lectotype: 860 µm); 813 µm (± 9) (800–820) ($n = 3$) (BMNH 1893.2.4.1991–1993, type lot of *Helicina vernalis*, lectotype: 820 µm).

Operculum (Fig. 62): Very slightly calcified, calcareous plate leaving a free margin, thickened towards the columellar side. Color reddish horny-amber, only the central area yellowish-transparent. Columellar side nearly regular S-shaped, upper end acute and pointed, lower end continuously changing into outer margin.

Animal (Figs. 337D, E): Foot and head are greyish and become darker towards the dorsal side; tentacles are greyish too. The mantle pigmentation shows a high variability: seldom unicolored light or dark, often basic color light yellowish with two (or seldom one) brown distinct but irregular bands on the last whorl above and below the periphery and more or less irregularly brownish spotted throughout the mantle. The few specimens from Arenal were only brownish spotted with small dots. The pattern is almost always clearly visible through the shell.

Radula (Fig. 63): A-central without well-defined cusps, B-central in most cases with 3–4, C-central only occasionally with up to 6 small cusps. Comb-lateral with 8–9 cusps, cusps on marginals slowly increasing in number. Radula with about 66–86 rows of teeth. Description agrees with Baker (1922a: pl. III, fig. 7, pl. IV, fig. 14).

Female Reproductive System (Figs. 64, 65): The receptaculum seminis is a small, simple drop-shaped sac, the bursa copulatrix pos-

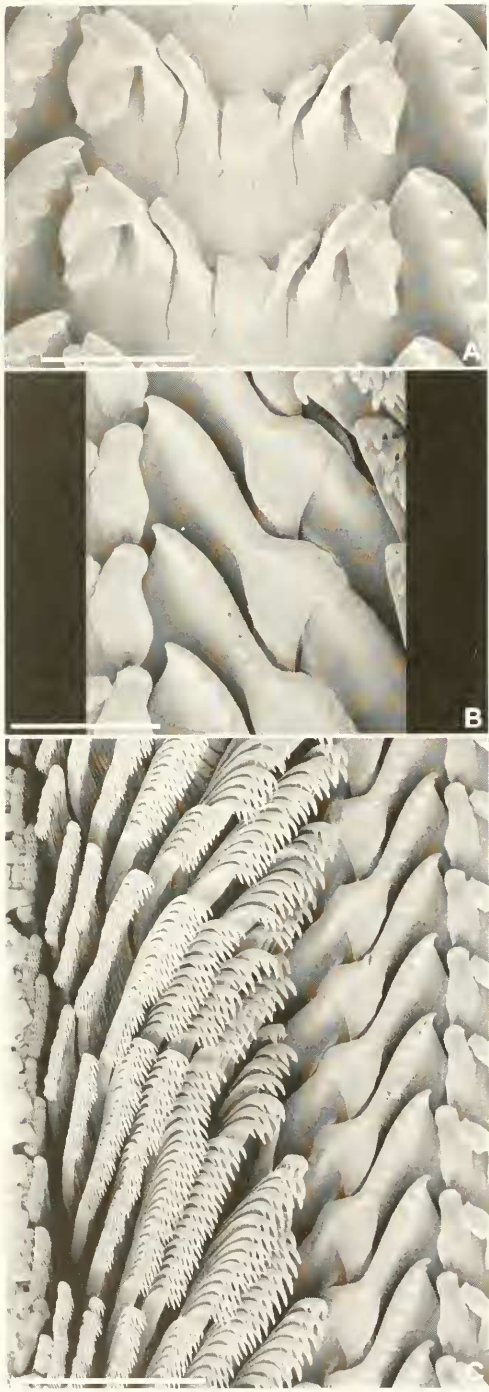


FIG. 63. Radula of *Helicina tenuis*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 μ m (A, B), 100 μ m (C).

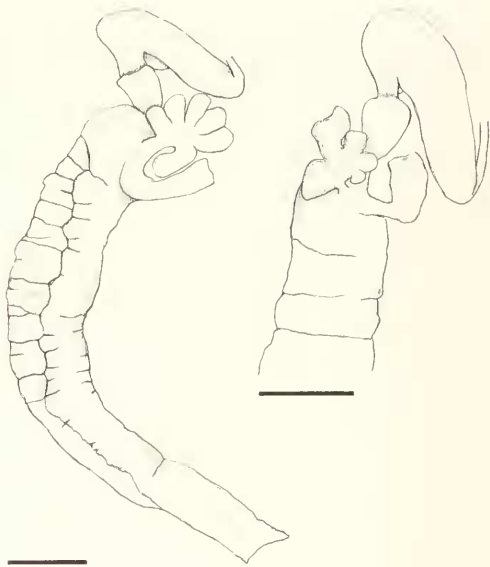


FIG. 64. Female reproductive system of *Helicina tenuis*, IR 1001; scale bar 1 mm.

sesses few rather large simple lobes and is of moderate size. The provaginal sac is oblong and well inflated, its distal end bears a few small processes. It has a slightly greyish-brownish pigmentation. The stalk is shorter than in *Helicina funcki* and rather stout.

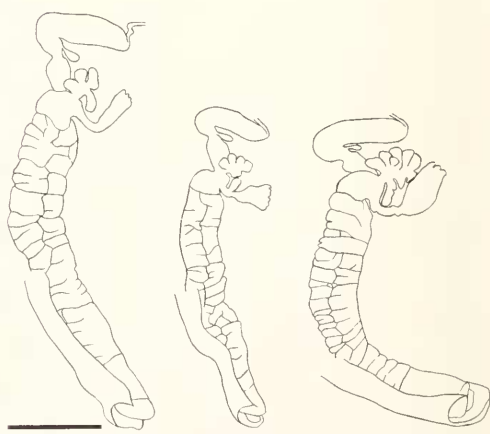


FIG. 65. Variability of the female reproductive system of *Helicina tenuis*, IR 1002; scale bar 2.5 mm.

TABLE 6. Measurements of different populations of *Helicina tenuis* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens; only population from "Cabo Blanco" and "La Selva" were determined for the sex (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

"Cabo Blanco" (altitude 30 m) lots IR 1001, IR 1002, IR 1289							"La Selva" (altitude 60 m) lots IR 1057, IR 1181				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	8.12	0.36	7.28	8.98	54	-	-	-	-	-
Height	m	7.34	0.25	6.71	7.92	30	8.23	0.27	7.83	8.67	4
Maj. diam.	f	7.93	0.29	7.18	8.69	54	-	-	-	-	-
Maj. diam.	m	7.33	0.19	6.90	7.72	30	8.06	0.21	7.75	8.36	4
Min. diam.	f	7.31	0.27	6.67	8.03	54	-	-	-	-	-
Min. diam.	m	6.68	0.18	6.33	7.00	30	7.38	0.14	7.15	7.55	4
Outer lip	f	5.39	0.24	4.81	6.05	54	-	-	-	-	-
Outer lip	m	5.03	0.16	4.49	5.99	30	5.53	0.16	5.37	5.70	4
Last whorl	f	6.43	0.29	5.64	7.24	54	-	-	-	-	-
Last whorl	m	5.83	0.21	5.47	6.24	30	6.39	0.23	6.15	6.67	4
Col. axis	f	6.37	0.26	5.65	7.12	54	-	-	-	-	-
Col. axis	m	5.74	0.19	5.01	6.23	30	6.50	0.18	6.13	6.73	4
Weight	f	0.030	0.009	0.015	0.092	54	-	-	-	-	-
Weight	m	0.027	0.007	0.013	0.048	30	0.053	0.011	0.037	0.065	3
Volume	f	0.159	0.018	0.119	0.207	54	-	-	-	-	-
Volume	m	0.117	0.010	0.100	0.136	30	0.162	0.011	0.145	0.172	3

"Diriá" (altitude 220–260 m) lots INBio 1498286, 1498287, 3096450						"Barra Honda" (altitude 100–300 m) lots INBio 1463452, 1463476				
	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	7.89	0.30	7.15	8.43	8	8.48	0.36	7.67	9.02	6
Maj. diam.	7.91	0.22	7.61	8.32	9	8.11	0.29	7.59	8.68	6
Min. diam.	7.14	0.20	6.82	7.48	9	7.55	0.26	6.98	7.98	6
Outer lip	5.19	0.18	5.00	5.85	8	5.50	0.21	5.23	5.43	6
Last whorl	5.99	0.19	5.66	6.36	8	6.42	0.41	5.60	6.93	6
Col. axis	6.27	0.20	5.73	6.68	9	6.88	0.36	6.03	7.34	6

"Cabo Blanco, INBio" (altitude 15–120 m) lots INBio 1465481, 1475801, 1475805, 1480012, 1484853, 1498272, 1498276, IR 1481						"Turrubares" (altitude 500 m) lot MHNN				
	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	7.94	0.39	6.92	8.68	22	7.88	0.50	6.91	9.00	21
Maj. diam.	7.95	0.35	7.00	8.60	22	7.90	0.41	7.20	8.80	21
Min. diam.	7.22	0.33	6.32	7.73	21	7.11	0.36	6.49	7.97	21
Outer lip	5.30	0.26	4.65	5.85	22	5.22	0.21	4.85	5.80	21
Last whorl	6.23	0.32	5.30	6.78	22	6.05	0.35	5.40	6.84	21
Col. axis	6.25	0.34	5.29	6.90	22	6.09	0.41	5.30	7.15	21

(Continues)

(Continued)

	"Carara" (altitude 100 m) lot INBio 3129469					"Osa" (altitude 60–545 m) lots INBio 1480502, 1484663, 1487328, 1487810				
	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	8.08	0.52	7.31	8.68	3	7.55	0.83	6.70	8.68	4
Maj. diam.	7.60	0.28	7.18	7.93	3	6.98	0.58	6.35	8.06	5
Min. diam.	7.10	0.39	6.51	7.60	3	6.54	0.57	5.88	7.35	4
Outer lip	5.28	0.39	4.70	5.67	3	4.95	0.38	4.51	5.74	5
Last whorl	6.21	0.27	5.81	6.60	3	5.99	0.58	5.44	6.86	5
Col. axis	6.22	0.46	5.53	6.88	3	6.00	0.69	5.24	6.85	4

Morphometry and Sexual Dimorphism

Although *Helicina tenuis* is widely distributed, only data from Costa Rica and the type lot or those of type lots of synonyms, respectively, were included, because the lots studied from other areas consisted of only a very few specimens. Except for "La Selva", the Costa Rican populations originated from the Pacific side. The only southern specimens are those summarized as "Península de Osa" and the holotype of *H. tenuis pittieri* (Table 6, Figs. 66–70).

Morphometry: Regarding the type lot of *Helicina tenuis*, the non-conspecificity of all specimens is confirmed in the measurements, especially in the height-diameter-relation. *Helicina tenuis pittieri* closely approaches the mean value of the type lot in all characteristics. The same is true for the type lot of *H. vernalis*, which is larger, but otherwise shows similar relations between the different measurements, additionally supporting the status as a synonym. Except for "Península de Osa", the Pacific populations are remarkably similar to each other in all characteristics. The specimens from Barra Honda have a bigger shell, which is more highly elevated (height, columellar

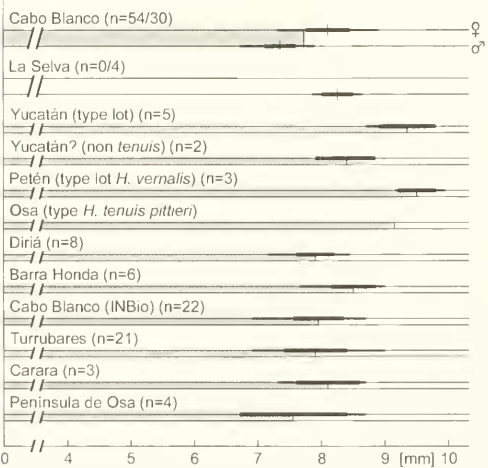


FIG. 66. Shell height of different populations of *Helicina tenuis* in Costa Rica according to Table 6; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males or total"; upper line: females, lower line: males if separate; in between and shaded: average of both for comparison with populations of unknown sex.

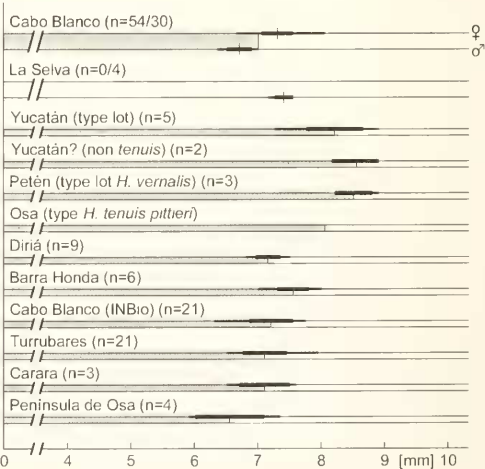


FIG. 67. Minor diameter of shell of different populations of *Helicina tenuis* in Costa Rica according to Table 6; for explanations see Fig. 66.

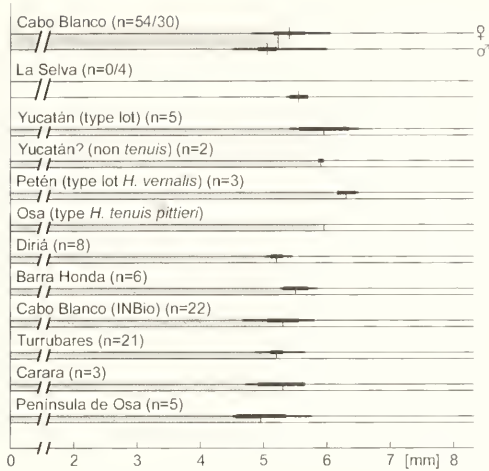


FIG. 68. Expansion of outer lip of different populations of *Helicina tenuis* in Costa Rica according to Table 6; for explanations see Fig. 66.

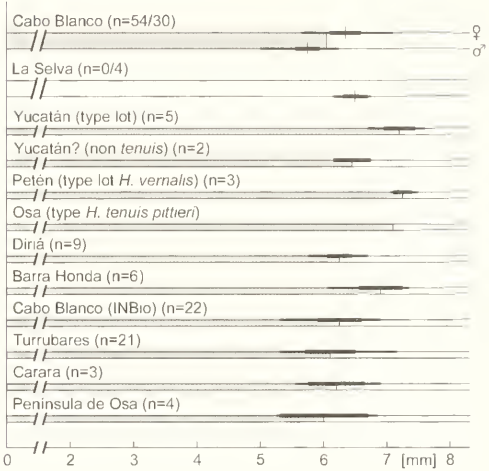


FIG. 70. Height of columellar axis of different populations of *Helicina tenuis* in Costa Rica according to Table 6; for explanations see Fig. 66.

axis). Besides the small sample size, the comparatively high deviations among the specimens from Península de Osa presumably reflect the fact that they originate from different sites on the Península and cannot be considered as a real population the same as the others. Contrary to their small size the type of *H. tenuis pittieri*, collected about 100

years ago on the same peninsula, is exceptional big for the Pacific populations. It suggests that *H. tenuis* displays greater size variation in this area, but the scanty material does not allow further conclusions.

Considering the sexual dimorphism, the average shell height of Caribbean specimens from "La Selva" can be estimated approximately 8.6 mm, thus being bigger than the Pacific populations. This may be caused by the drier climate on the northern Pacific side as compared to the Caribbean plain.

In general, the average of the type lot of *H. tenuis* appears to be typical for the Mexican and Guatemalan areas, since many single specimens from this region were measured and approach a similar size. Nevertheless, smaller specimens were also present, as was the case for the type lot that also may have consisted of specimens from various localities in Yucatán. Goodrich & van der

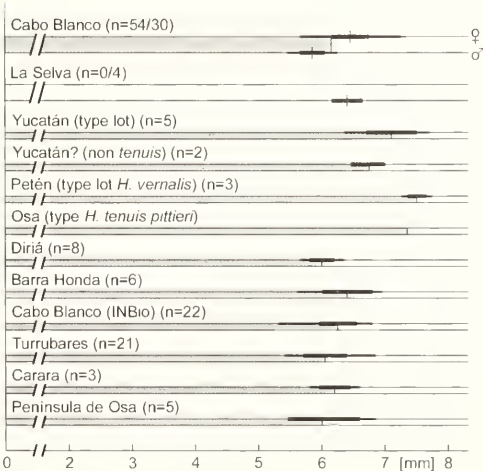


FIG. 69. Height of last whorl of different populations of *Helicina tenuis* in Costa Rica according to Table 6; for explanations see Fig. 66.

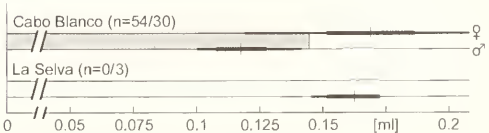


FIG. 71. Shell volume of different populations of *Helicina tenuis* in Costa Rica according to Table 6; for explanations see Fig. 66.

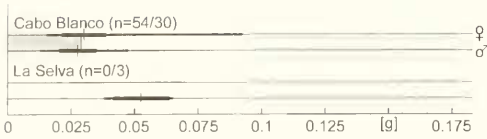


FIG. 72. Shell weight of different populations of *Helicina tenuis* in Costa Rica according to Table 6; for explanations see Fig. 66.

Schalie (1937) state for Péten and North Alta Verapaz, northern Guatemala, that shells from the southern region are a little smaller, unfortunately without giving any measurements. In conclusion, it can be assumed that the shell size of *H. tenuis* varies throughout the whole range of distribution, obviously depending on environmental factors. Near its southern limit of distribution in Costa Rica, the average size is smaller.

Sexual Dimorphism: The 84 specimens of the Cabo Blanco population show clear differences with the average size of females larger than males. The measurements overlap, as shown for height and minor diameter in Fig. 73, but to a smaller degree than in *H.*

funcki (Fig. 32). As may be expected, the volume (Fig. 71) best reflects the differences, the average volume of male amounts only 73.6% of the females. The shell weight of both sexes is nearly equal (Fig. 72), therefore males possess relatively heavier shells (Fig. 74).

Habitat

During this study, *Helicina tenuis* was only found in comparatively high abundance during the rainy season in the Cabo Blanco reserve. During the daily rains, the snails were seen crawling on and under living and dead leaves of bushes and palms and on stems. None were collected on the ground. In the same place, *H. tenuis* was nearly "absent" during the dry season, except for very few specimens that were aestivating in folded palm leaves. Two of these seven specimens found were visibly parasitized by larvae of trematodes, whereas no other helicínids ever were found to be infected in this obvious way. It is not clear where the majority of specimens retreat to during the dry period. In addition to the arboreal habitats, searches were conducted in the leaf litter and around the stems of bushes

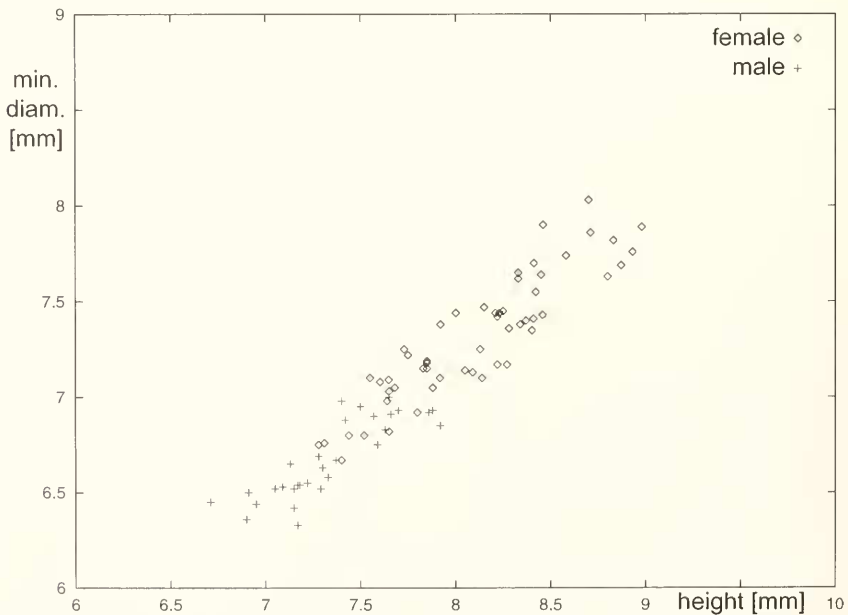


FIG. 73. Range of measurements in females and males exemplary for height and minor diameter in the population from Cabo Blanco.

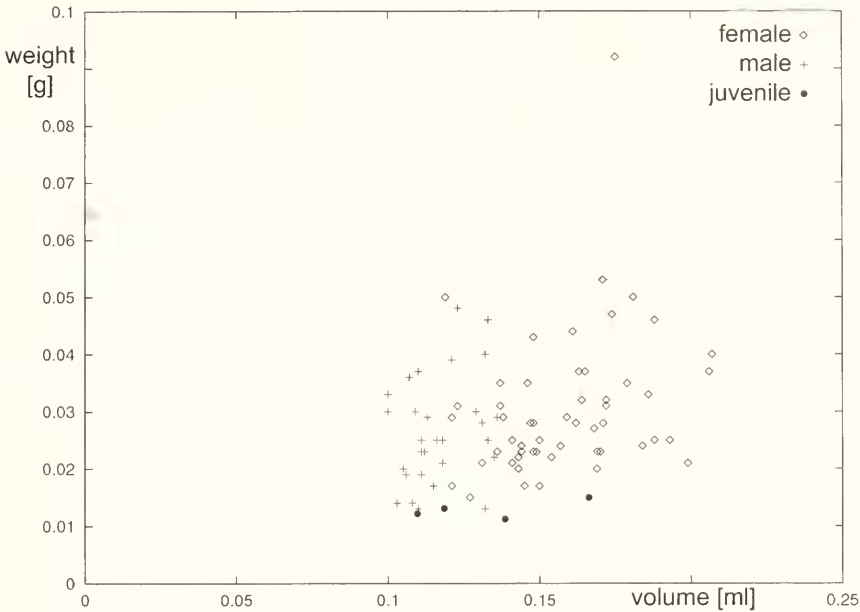


FIG. 74. Relation of weight to volume in females and males of the populations from Cabo Blanco.

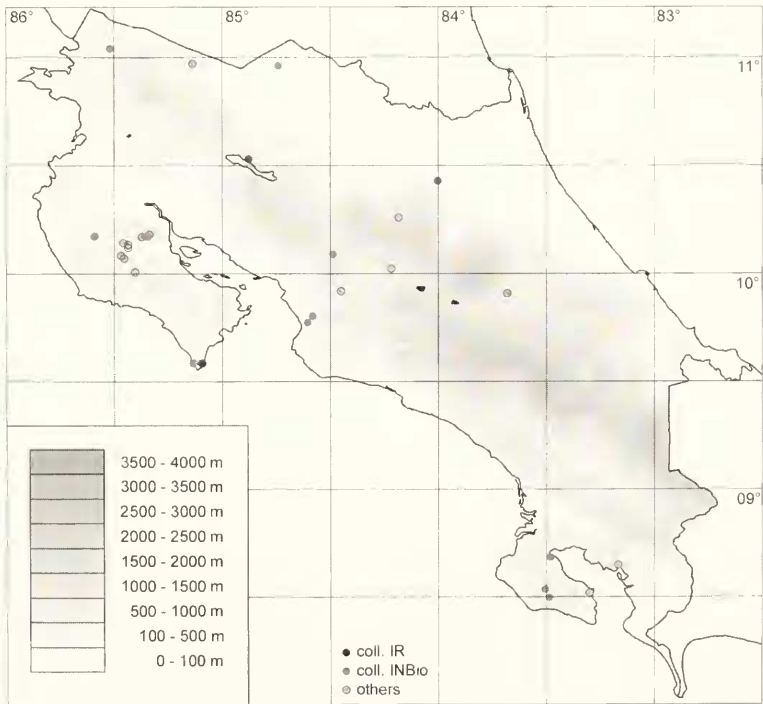


FIG. 75. Records of *Helicina tenuis* in Costa Rica.

and palms on the ground but without success. In other areas without such contrasting seasonal changes (e.g., near Nuevo Arenal, La Selva), *H. tenuis* was only found occasionally during the dry as well during the rainy season. There it was additionally found on the underside of leaves of Musaceae or Heliconiaceae, respectively, which are absent in the drier Cabo Blanco area.

These habitats correspond to those observed by Biolley (1897) for Costa Rica and Baker (1922b) from southern Veracruz in Mexico, who additionally found the species "on the ground and on leaves of shrubs and cacti in the savannah forests". Van der Schalie (1940) reported *H. tenuis* from Alta Verapaz in Guatemala as common and as being found near Panzamal "moving about on the vegetation at night".

With its occurrence on the Península de Nicoya, *H. tenuis* tolerates the highest level of dryness among the Costa Rican Helicinidae and is the only species that can withstand the regular extended dry period during the year. As cited above, it also inhabits the Savannah in association with cacti. This comparatively high ecological tolerance of *Helicina tenuis* among the Helicinidae provides a possible explanation for its remarkably wide distribution.

Distribution

The species reaches its northern limit in southern Mexico (states of Guerrero, Oaxaca, Veracruz) and occurs throughout Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica to western Panama. Even more northern sites in Central Mexico (states of Jalisco and Guanajuato) were listed by von Martens (1890–1901), but the specimens have not been re-examined. The most southeastern record comes from the Tonosi, Los Santos Province, Panama (Pilsbry, 1926a). The specimens from Isla Barro Colorado in the Canal Zone of Panama (Pilsbry, 1930) seem to belong to another species (see "Discussion"). *Helicina tenuis* is found on the Caribbean as well as on the Pacific side of the central mountain chains. Except for *Lucidella lirata*, it is thus probably the most widely distributed species of Helicinidae of the Central American mainland.

In Costa Rica, the species is not common, but was nevertheless found at several distinct localities (Fig. 75). According to the collec-

tions, it seems to occur in relatively greater numbers in the Pacific plain, where it also appears to be more widely distributed. Compared with areas investigated and inhabited by other helicinids (e.g., see *H. funcki*), the apparent lack of *H. tenuis* on the Caribbean side at many localities is remarkable, because the species is found in a similar habitat and is comparatively large. In fact, it is completely absent throughout the large province of Limón stretching along the entire Caribbean coast of Costa Rica. La Selva and Turrialba represent the most southeastern localities.

Discussion

The nomenclatural discussion of *Helicina tenuis* is complicated because several confusions have arisen and been maintained in literature.

First, it is important to note that *Helicina tenuis* is not preoccupied by *Helicina tenuis* C. B. Adams, 1849 (now *Stoastomops adamsi* Baker, 1934) from Jamaica, because the latter name was published in September 1849 (Baker, 1934a) and not as stated by von Martens (1890) or Bequaert & Clench (1933) in 1840.

Traditionally, *Helicina tenuis* and *H. lindeni*, both described by L. Pfeiffer in the same paper, the second one page before the other, are regarded as synonyms or varieties of one species. Sowerby (1866) only mentions *H. lindeni*, and his drawing probably represents *H. tenuis*, but both figure and the very short paragraph on the species do not provide sufficient information to assess the status. Von Martens (1890: 34–35) proposed the synonymy without further explanation, except for a statement about the figure of *H. lindeni* in L. Pfeiffer (1850) "not good", and he used *H. tenuis* as the valid name, which also would have established priority because von Martens was the first revising author. Fischer & Crosse (1893) agreed upon the conspecificity, but claimed that *H. lindeni* had page priority and *H. tenuis* became a variety. None of these authors mentions an investigation of the original material (Fischer & Crosse did so for *H. vernalis*), nor did they give reasons for their opinion. Interestingly enough, von Martens (1900: 604) replied in his supplemental part to the French authors, regarding *tenuis* as the most applicable name and remarked on the rather great distinctness L. Pfeiffer attributes to these species (see below). Because both publications

are standard contributions on terrestrial molluscs for Central America, subsequent authors used the one or other name, but commonly adopted the synonymy.

L. Pfeiffer (e.g., 1852a: 372, 388) assigned his two species to different higher groups ("§. 8. Ecarinatae" [*H. tenuis*] and "§. 10. Subcarinatae" [*H. lindeni*]). The descriptions and the subsequently published figures (L. Pfeiffer, 1850) (reprinted here in Fig. 76) are in fact not similar enough to support the synonymy. Obvious differences can be summarized in a less elevated shell in *H. lindeni* ("globosa-conica" instead of "turbinata"; "spira acutiuscula" instead of "acuta" and the measurements). Furthermore, *H. lindeni* is slightly angulated and does not bear color bands, the outer lip is "breviter expanso, reflexiusculo" instead of "tenui, angulatim expanso". L. Pfeiffer's descriptions are short, but very precise in certain details. Regarding the literature, the conclusions of von Martens and Fischer & Crosse can thus not be understood, especially the "not good" figure of *H. lindeni*, because it perfectly matches the written description. Since the type material of *H. lindeni* is still unavailable, possible deviations of the original material (perhaps seen by other authors) from the description that could have explained those conclusions, remain subject to speculation. A variety of *H. lindeni* from the Cuming collection (BMNH 20010757) fits well to the description and figure of *H. lindeni*. In conclusion, *H. tenuis*, for which a lectotype could be chosen in full agreement with the description and the current interpretation, is regarded as specifically distinct from *H. lindeni*. The Costa Rican specimens clearly belong to *H. tenuis*. According to comments and figure *H. lindeni sensu* Fischer & Crosse (1893) is synonymous with *H. tenuis*.

The type material of *Helicina vernalis* and *H. chiapensis* was investigated and the species are confirmed as synonyms of *H. tenuis*. The taxon *H. vernalis verapazensis* proposed by Wagner (1905) was included into the synonymy of *H. tenuis* by himself.

The present status of *Helicina tenuis pittieri* is doubtful, because comparable material from the Peninsula de Osa is very scarce and the few specimens available show a high variation in size, are always not only smaller, but also belong to different sites. A common feature is the whitish band at the periphery, which is lacking in other Costa Rican populations. Considering the high variation of the widespread *H. tenuis* and the lack of further distinguishing characteristics, *H. tenuis pittieri* is tentatively regarded as a synonym. Wagner (1910a: 303), judging *H. tenuis* as variable and even not constant in local forms, presents only the new subspecies at the southern limit of the distribution as a "auffallender unterschiedene und anscheinend konstante Form" [strikingly different and apparently constant form]. According to the original description and as far as it could be traced in collections (ZMB, SMF, MIZ [Wagner coll.]), it seems very likely that he only knew a single specimen, the holotype of the so-called "constant form". More northern records in Costa Rica Wagner included in the nominal form.

Several records of *H. tenuis* from high elevations (e.g., Cerro Zunil) given by von Martens (1890–1901) likely refer to *H. punctisulcata zunilensis*, in one example cited it is very likely that the record exactly originates from the specimen on which Wagner (1910a) based his new subspecies. The record from the Canal island of Panama (Pilsbry, 1930) seems to be based on another species, because the size of the specimen (5/5.4 mm) is clearly beyond the range of *H. tenuis*.

The record of *H. oweniana* for Costa Rica by Monge-Nájera (1997) was checked in the INBio collection. The lots INBio 1463452 and 1464319 clearly determined before 1997, have to refer to *H. tenuis*. *H. oweniana* is finally distinguished from *H. tenuis* by its orange colored outer lip, a more solid shell, a less impressed suture with its lower margin whitish. *Helicina oweniana* lacks the typical denticle at the transition from the outer lip to the columella.

***Helicina (Tristramia) echandiensis*
Richling, n. sp.**

Type Material

Holotype: INBio 3542520, female (leg. Alexander Alvarado Mendez, 14.11.2001)



FIG. 76. Reproduction of the figures from L. Pfeiffer (1850) of A. *Helicina tenuis*. B. *Helicina lindeni*.



FIGS. 77, 78. *Helicina echandiensis* n. sp. FIG. 77. Holotype, INBio 3542520, height 7.2 mm. FIG. 78. Paratype 1, INBio 3542521, height 6.5 mm; scale bar 2.5 mm.

Paratype: INBio 3542521, male (same data as holotype)

Additional paratypes: INBio 3428246: 6 ads., 1 s.ads., 9 juvs., INBio 3574064: 1 s.ad. (same data as holotype)

Dimensions:

Holotype: 7.2/6.8/7.3/6.2/4.4/5.3/5.4 mm

Paratype 1: 6.5/6.1/6.5/5.7/3.9/4.8/5.1 mm

Type Locality

S-Costa Rica, Puntarenas Province, Parque Nacional La Amistad, Sector Las Alturas, Southern Cordillera de Talamanca, S of Cerro Echandi, campamento Echandi, 09°01'33"N, 82°49'12"W, 2,840 m a.s.l.

Etymology

The name refers to the origin of the species, the Cerro Echandi.

Examined Material

INBio COLLECTION

Puntarenas: Zona Protectora Las Tablas, sector Las Alturas, campamento de los nacientes del Río Vella Vista, 08°59'39"N, 82°49'18"W, 2,100 m a.s.l.: leg. E. Alfaro, 13.11.2001: 1 ad. (INBio 3505804)

Description

Shell (Figs. 77, 78, 335J–K): conical, thin and fragile, medium to small sized, only slightly shiny to dull. Color: basic color light orange-brownish; apex and upper whorl unicolored, only lighter towards the suture, about the 1.5 last whorls above periphery with a pattern of irregular, mostly parallel distinct white stripes in the same orientation as growth lines, about as wide as interspaces; stripes starting at suture and all ending at the same level a little above periphery. Surface textured with irregular growth lines and oblique grooves of different individual orientation but of same general direction (Fig. 80), causing the rather dull appearance. Embryonic shell with about 1 whorl; $3\frac{7}{8}$ ($3\frac{1}{2}$ –4) subsequent whorls very straight; last whorl also straight

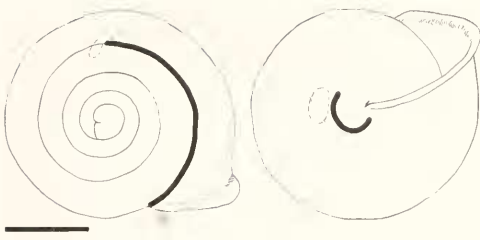


FIG. 79. Axial cleft and muscle attachments of *Helicina echandiensis* n. sp., INBio 3542520; scale bar 2.5 mm.

above and round at periphery and below; whorls equally extending in size, forming a very regular, pointed spire. Suture very slightly impressed. Aperture slightly oblique and straight, last whorl very slightly ascending towards the aperture and inserting just below the periphery. Outer lip of a bright orange, thickened, moderately and equally expanded. Reflection nearly rectangular to the whorl; transition to columella forming a blunt edge with a very small denticle. Columella oblique and rather straight, transition to the body whorl smooth. Basal callus weakly developed, at the base more pronounced and granulated.

Internal Shell Structures: (Fig. 79)

Teleoconch Surface Structure: *Helicina echandiensis* n. sp. seems to lack the transitional pattern (Fig. 80A), the whole teleoconch exhibits a structure of oblique diverging grooves (Fig. 80B). About the upper half of the beginning of the 1st whorl is occasionally sculptured with fine wrinkles parallel to the growth lines. Overlapping equally spaced periostracal spiral ridges also begin immediately at the teleoconch (Fig. 80A, arrow).

Embryonic Shell (Fig. 81): Faced with the paucity of material for *Helicina echandiensis* n. sp., only one specimen was studied under the SEM (INBio 3574064). The younger part of the embryonic shell appears compressed, as if it developed in slower growth, but this is not likely to be a typical feature. It is probably not related to living conditions at high altitudes where the species is found, because the embryonic shell of *H. punctisulcata*

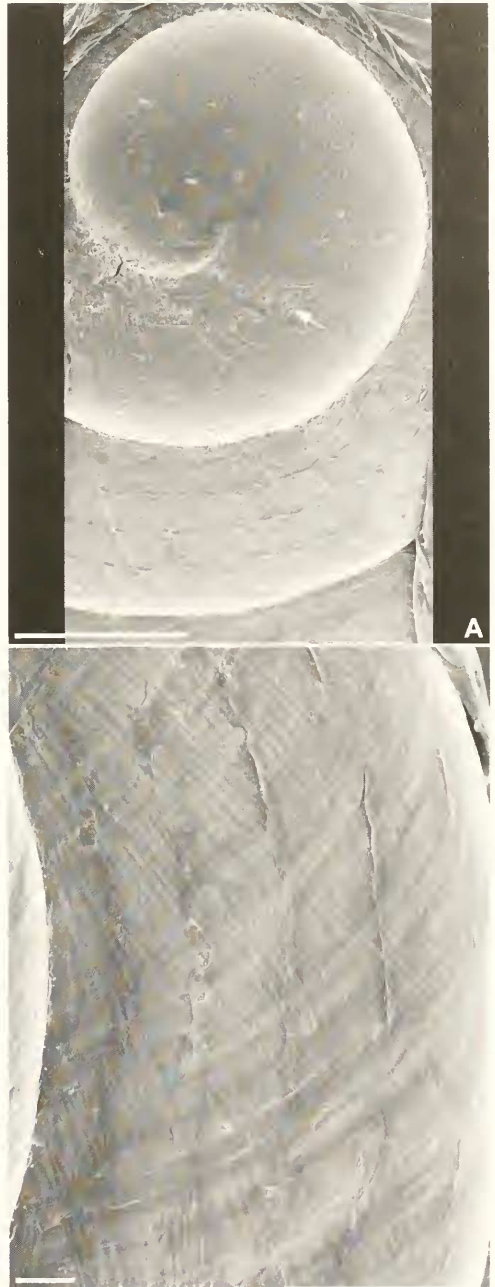


FIG. 80. Teleoconch surface structure of *Helicina echandiensis* n. sp. A. Embryonic shell and begin of 1st and 2nd whorl, arrow indicates exemplarily an early spiral ridge. B. 3rd whorl; scale bars 500 μ m (A), 100 μ m (B).



FIG. 81. Embryonic shell of *Helicina echandiensis* n. sp.; scale bar 100 μ m.

cuerciensis n. subsp. is normally developed. The arrangement of the pits is less regular than in the previous species, and the pits are relatively smaller. The embryonic shell size is much larger than in *H. escondida* n. sp. of equal shell size and even exceeds that of specimens of *H. funcki* from the lowlands. Diameter: 1,026 μ m (\pm 36) (960–1,120) (n = 9) (INBio 3428246, INBio 3542520, INBio 3542521).

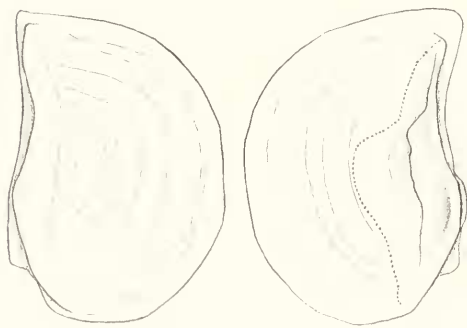


FIG. 82. Operculum of *Helicina echandiensis* n. sp., INBio 3542520; scale bar 1 mm.

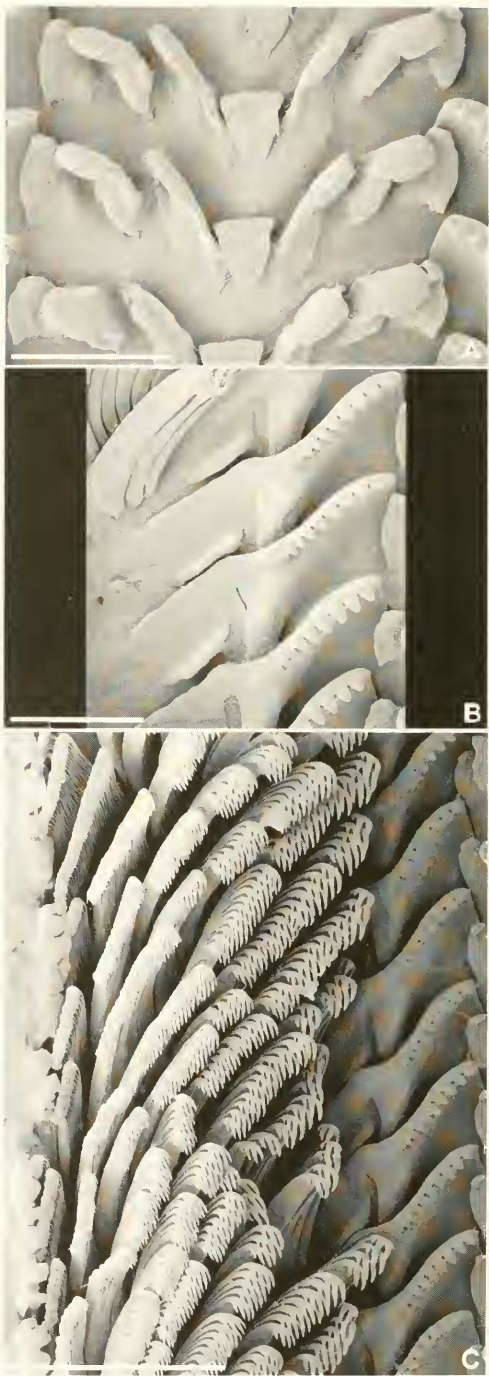


FIG. 83. Radula of *Helicina echandiensis* n. sp. A. Centrals. B. Comb-lateral. C. Marginals; scale bars 50 μ m (A, B), 100 μ m (C).

Operculum (Fig. 82): very slightly calcified, calcareous plate covering only part of outer surface. Color horny-amber to orange, only near the columella whitish or transparent. Columellar side slightly irregular S-shaped, upper end acute and pointed, lower end continuously changing into outer margin.

Animal: In the preserved specimens, the soft body is greyish-blackish throughout. Only towards the sides and underside of the foot does the color become lighter. The sides of the foot and parts of the mantle are occasionally only spotted greyish.

Radula (Fig. 83): Due to the lack of material, the radula of only one specimen was investigated. Cutting edges in centrals rather crenulate than bearing cusps, comb-lateral with 10–11 cusps, cusps on marginals slowly increasing in number. Radula with 72 rows of teeth.

Female Reproductive System (Fig. 84): The receptaculum seminis is long and slender and joins the descending limb of the V-organ at the middle of its inner side. The bursa

copulatrix is moderately lobed, the flattened provaginal sac is of about equal size. It is clearly demarcated from its short and stout stalk, the distal side is irregularly subdivided. The pallial oviduct is mainly transversally constricted.

Morphometry and Sexual Dimorphism (Table 7, Fig. 85)

The material available is very limited, but because the sex of all these eight adult specimens could be determined (two by removal from the shell, the rest by external inspection enabled by the transparency of the shells), it seems worthwhile including them in the data.

The measurements show a range of deviations that is higher than in the populations of the similarly sized *Helicina escondida* n. sp. for which a comparable number of specimens was analyzed. A sexual dimorphism is indicated with the females being bigger than the males, but the data overlapping slightly. The differences for height and minor diameter in females and males amount less than in such species as *H. gemma* and *H. beatrix* and resemble those of *H. escondida* n. sp. In interpolation from the minor diameter, males have a volume of about 75% that of females.

Habitat

The type locality is located in an area characterized by montane rain forest. The field notes of Alexander Alvarado Mendez state that the specimens were found in very humid, primary



FIG. 84. Female reproductive system of *Helicina echandiensis* n. sp., INBio 3542520; scale bar 1 mm.

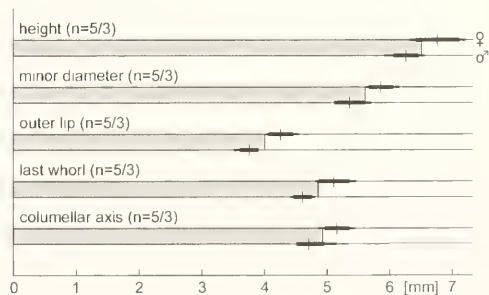


FIG. 85. Measurements of *Helicina echandiensis* n. sp. according to Table 7; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males"; upper line: females, lower line: males; in between and shaded: average of both.

TABLE 7. Measurements of *Helicina echandiensis* n. sp. given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm].

"Cerro Echandi" (altitude 2840 m) lots INBio 3428246, 3542520, 3542521						
	Sex	Mean value	Deviation	Min	Max	Number
Height	f	6.75	0.34	6.28	7.18	5
Height	m	6.24	0.22	5.92	6.53	3
Maj. diam.	f	6.40	0.23	6.02	6.81	5
Maj. diam.	m	5.78	0.21	5.50	6.10	3
Min. diam.	f	5.87	0.22	5.59	6.15	5
Min. diam.	m	5.34	0.23	5.08	5.68	3
Outer lip	f	4.27	0.19	4.00	4.55	5
Outer lip	m	3.75	0.16	3.52	3.92	3
Last whorl	f	5.09	0.25	4.78	5.45	5
Last whorl	m	4.62	0.14	4.41	4.79	3
Col. axis	f	5.15	0.22	4.86	5.44	5
Col. axis	m	4.79	0.23	4.50	5.13	3

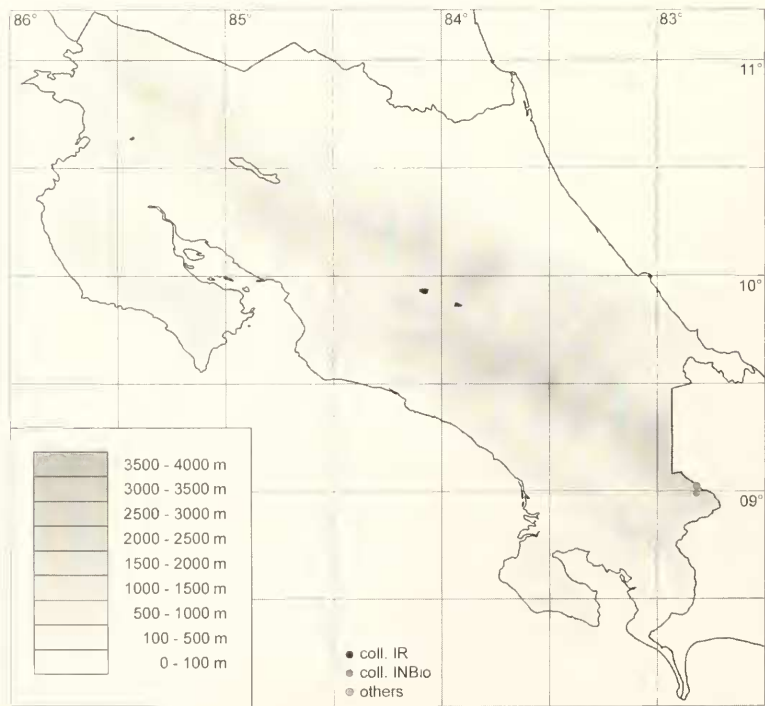


FIG. 86. Records of *Helicina echandiensis* n. sp. in Costa Rica.

forest on black soil. The undergrowth mainly consisted of Heliconiaceae. Considering the shell color and the habitats of comparable species, it seems likely that *Helicina echandiensis* n. sp. was also found on these plants.

Distribution (Fig. 86)

Helicina echandiensis n. sp. is known only from the southern slopes of Cerro Echandi a little below the summit, from altitudes of 2,100 to 2,840 m. The area is part of the central mountain chain of the Cordillera de Talamanca.

Discussion

Helicina echandiensis n. sp. is unique in its combination of characteristics. It can be distinguished from the other species with a bright reddish-orange outer lip – *H. gemma*, *H. beatrix riopejensis* n. subsp. – by the straight and uncurved form of the latter and the surface structure of oblique diverging grooves. Among helicids of this shape and shell surface texture it is comparable in size only to *H. escondida* n. sp., which has a light yellowish outer lip, a less pronounced surface structure, and more convex whorls. Furthermore *H. escondida* n. sp. lacks the characteristic diagonal white stripes and seems to be restricted to the Caribbean side of the central mountain chains.

***Helicina (Tristramia) punctisulcata*
cuerciensis
Richling, n. subsp.**

Type Material

Holotype: INBio 3542622 (leg. A. Picado, 19.01.1996)

Paratype: INBio 3542541, female (09°33'19"N, 83°40'13"W, 2,600 m a.s.l.: colectado

mediante sombrereta [collected by beating vegetation], leg. B. Gamboa, 29.10.1995)

Dimensions:

Holotype: 5.9/6.5/6.8/5.8/4.1/4.4/4.8 mm

Paratype: 7.9/7.3/7.7/6.8/4.5/5.6/6.5 mm

Type Locality

Central Costa Rica, San José Province, Cordillera de Talamanca, Estación Cuerici, 4.5 km E de Villa Mills, Sendero el Mirador, 09°33'28"N, 83°40'13"W, 2,700 m a.s.l.

Type Material of Relevant Taxa

Helicina punctisulcata von Martens, 1890

Helicina punctisulcata von Martens, 1890: 36–37, pl. I, fig. 10

Type Material: Lectotype ZMB 103326a: leg. H. H. Smith, additional paralectotypes ZMB 103326b, ZMB 103326c, ZMB 103325

Von Martens based the description on material collected by H. H. Smith, which is in the collection of the ZMB. Four specimens from ZMB 103326 were marked to be figured by von Martens, of which only one matches the measurements given in the original description, the other being much smaller (about 1.3 to 1.8 mm smaller in the greater diameter). Furthermore, it best fits his upper right basal view, with a minute groove in the columellar region. This specimen is **herein selected as lectotype** (Fig. 87).

Dimensions (height/greatest diameter/minor diameter):

Lectotype: 7.2/8.9/7.8 mm

Type Locality: "W Mexico: Omilteme, 8000 ft. on the Sierra Madre del Sur, State of Guerrero, Pacific side of the main cordillera"



FIG. 87. *Helicina punctisulcata*, lectotype, ZMB 103326a, height 7.2 mm; scale bar 2.5 mm.

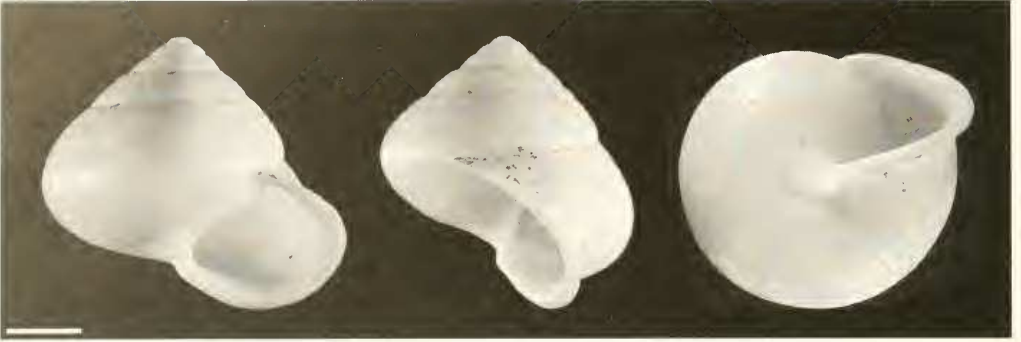


FIG. 88. *Helicina punctisulcata zunilensis*, holotype, ZMB 103324, height 9.2 mm; scale bar 2.5 mm.

Helicina punctisulcata zunilensis Wagner, 1910

Helicina punctisulcata zunilensis Wagner, 1910a: 295, pl. 59, fig. 9

Type Material: Holotype ZMB 103324

Because the original description refers to one specimen in the museum in Berlin, the

single specimen matching the figure is the holotype (Fig. 88).

Dimensions (height/greatest diameter/minor diameter):

Holotype: 9.2/10.2/8.7 mm

Type Locality: "Vulkan Zunil in Guatemala" [Guatemala, at border of Quezaltenango and Solola departments, volcano Volcán Zunil]



FIGS. 89, 90. *Helicina punctisulcata cuericiensis* n. subsp. FIG. 89. Holotype, INBio 3542622, height 5.9 mm. FIG. 90. Paratype, INBio 3542541, height 7.9 mm; scale bar 2.5 mm.



FIG. 91. Axial cleft and muscle attachments of *Helicina punctisulcata cuericensis* n. subsp., INBio 3542622; scale bar 2.5 mm.

Etymology

The name refers to the origin of the species, the Cerros Cuerici.

Examined Material

INBio COLLECTION

San José: *Estación Cuerici: Sendero el Mirador*, 4.5 km E de Villa Mills, 09°33'28"N, 83°40'13"W, 2,700 m a.s.l.: leg. A. Picado, 19.01.1996 (INBio 3542622); 19.01.1996 (INBio 3542527); colectado en una planta [collected on a plant] 26.06.1996, leg. B. Gamboa (INBio 3544828); 2,750 m a.s.l.: leg. A. J. Mora, 27.11.1995 (INBio 3542528); 09°33'19"N, 83°40'13"W, 2,600 m a.s.l.: colectado mediante sombrereta [collected by beating vegetation], leg. B. Gamboa, 29.10.1995 (INBio 3542541); recolectado en una rubiaceae caminando [collected crawling on a Rubiaceae], leg. A. Picado, 26.08.1995 (INBio 3542539)

Description

Shell (Figs. 89, 90, 335L–M): Conical, solid, medium to small sized and only slightly shiny to dull. Color: apex and upper whorl dark yellow, becoming lighter with growth and increasingly whitish spotted, towards the aperture changing to whitish with small yellowish spots. Surface textured with irregular growth lines and oblique grooves of different individual orientation but of the same general direction (Fig. 92), causing the dull appearance; last two whorls with 3–4 equally spaced spiral grooves. Embryonic

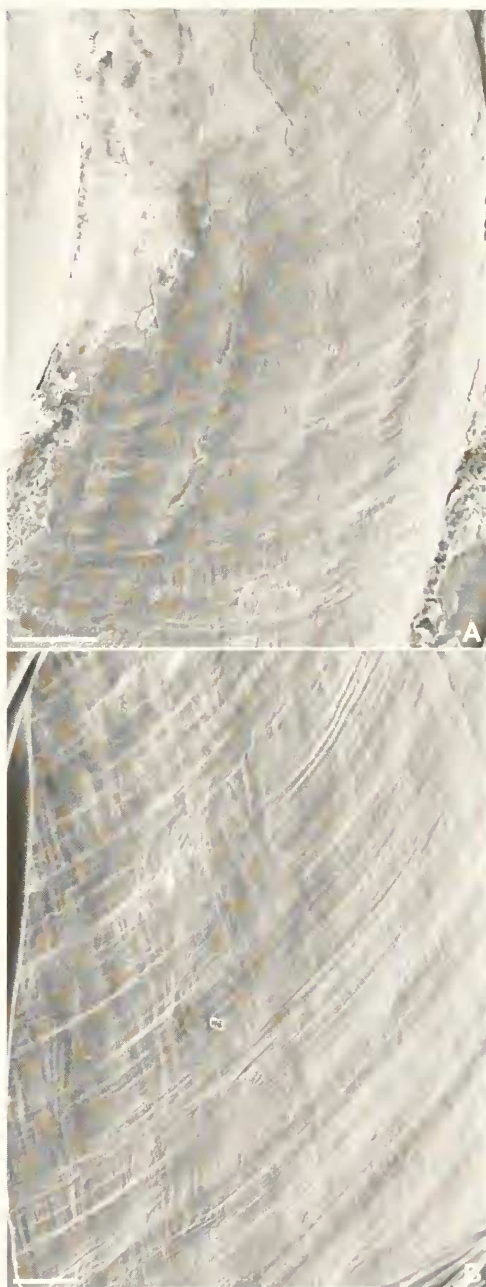


FIG. 92. Teleoconch surface structure of *Helicina punctisulcata cuericensis* n. subsp. A. 2nd whorl, partly eroded. B. 4th whorl; scale bar 100 μ m.



FIG. 93. Embryonic shell of *Helicina punctisulcata cuericiensis* n. subsp.; scale bar 100 μ m.

shell with about 1 whorl; $3\frac{5}{8}$ ($3\frac{5}{8}$ – $4\frac{1}{2}$) subsequent whorls straight, the last whorl very slightly angulated at the periphery and rounded below; whorls equally extending in size, forming a very regular, pointed spire. Suture moderately impressed. Aperture oblique and straight, last whorl slightly descending towards aperture and inserting below the periphery. Outer lip yellowish, re-

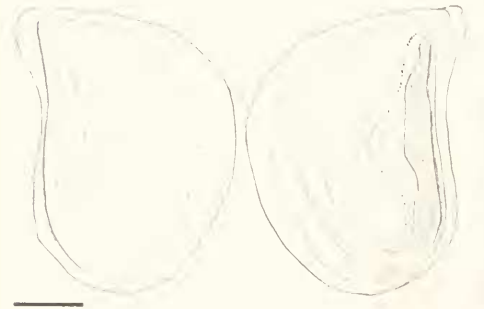


FIG. 94. Operculum of *Helicina punctisulcata cuericiensis* n. subsp., INBio 3542622; scale bar 1 mm.

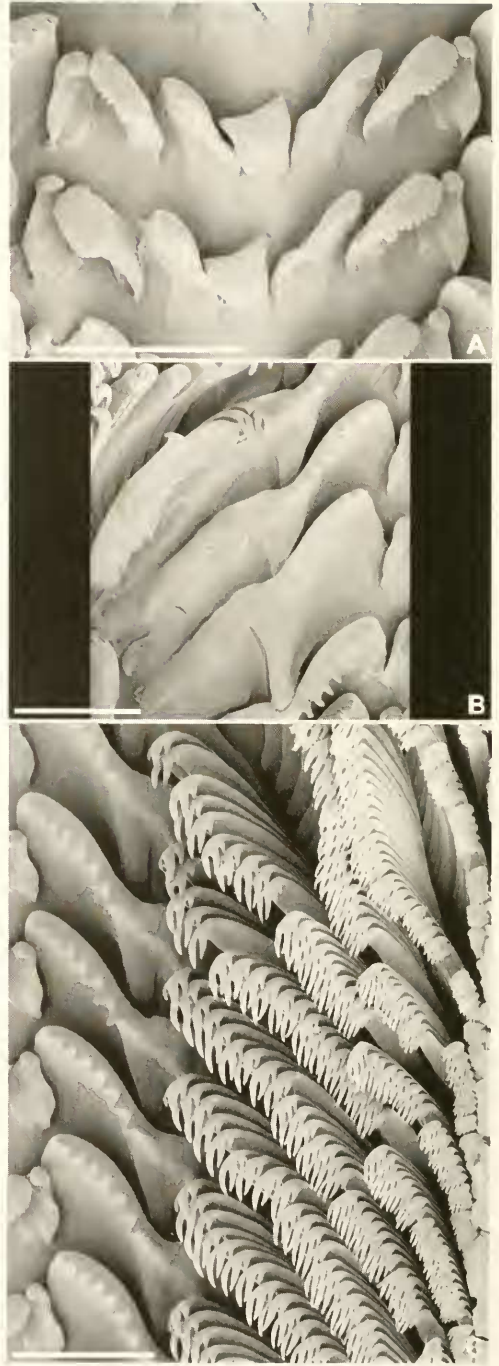


FIG. 95. Radula of *Helicina punctisulcata cuericiensis* n. subsp. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 μ m.

markably thickened and equally expanded, edge appearing rounded. Transition to columella protruding, forming a blunt edge with a denticle. Columella very short and curved, transition to the body whorl with sharply impressed line. Basal callus well developed, very pronounced in umbilical area and finely granulated.

Internal Shell Structures: (Fig. 91)

Teleoconch Surface Structure (Fig. 92): In all of the few available specimens, the beginning of the teleoconch is eroded. On the second whorl, the surface is sculptured with oblique diverging grooves continuing throughout the whole teleoconch. This pattern is interposed with distinct, irregular growth lines (Fig. 92B) and spiral grooves, which are characteristic for *Helicina punctisulcata cuericiensis* n. subsp.

Embryonic Shell (Fig. 93): Only a single specimen could be studied. The structure is similar to that of *Helicina funcki*. As in *H. echandiensis* n. sp. the diameter is relatively very large.

Diameter: 1,038 μm (± 15) (1,000–1,060) ($n = 5$) (INBio 3544828, 3542541, 3542539, 3542528, 3542622).



FIG. 96. Female reproductive system of *Helicina punctisulcata cuericiensis* n. subsp., INBio 3542528; scale bar 1 mm.

Operculum (Fig. 94): Very slightly calcified, calcareous plate covering only part of the outer surface. Color horny-amber, at nucleus nearly transparent. Columellar side slightly regularly S-shaped, upper end acute and pointed, lower end rounded, but slightly truncated.

Animal: In preserved specimens, the soft body is greyish-black throughout, only towards the sides and underside of the foot the color becomes lighter to whitish-yellowish. The dark color of the mantle gives the shells of live specimens a greenish tinge.

Radula (Fig. 95): Only two specimens were investigated. The B-central bears 8 well defined cusps, whereas A- and C-central may be a little crenulated. Comb-lateral with 8–11 cusps, cusps on marginals slowly increasing in number. Radula with about 60 rows of teeth.

Female Reproductive System (Fig. 96): The V-organ is comparatively slender, the oblong receptaculum seminis joins its descending limb about the middle of the inner side. The bursa copulatrix is relatively large and compact, it is subdivided in a few simple lobes. The provaginal sac is oblong and finely irregularly lobed at its distal side, a stout, short duct continues to the reception chamber. The sac is blackish pigmented.

Morphometry and Sexual Dimorphism

The amount of material is too limited to be analyzed. The shape of the holotype is representative for all other specimens except for the paratype, which is higher elevated and more evenly rounded at the periphery. The holotype is the smallest specimen, whereas the paratype is the largest.

Two specimens dissected for anatomical studies are females, of which one is the paratype. The other specimen represents the smallest of the four live-collected individuals.

Habitat

The field notes from the collectors of INBio indicate that the species climbs on vegetation, where it was found "en una rubiaceae caminando [crawling on a Rubiaceae]" or by beating vegetation. The type locality is situated in a transitional zone of montane rain forest to paramó vegetation.

Distribution (Fig. 97)

Helicina punctisulcata cuericiensis n. subsp. is only recorded from the main ridge of the northern Cordillera de Talamanca west of the Cerros Cuerici.

Discussion

The specimens were tentatively classified as a new subspecies of *Helicina punctisulcata* because of the resemblance to this species and its subspecies *H. p. zunilensis* in the shell surface structure, color, shell thickness, and development of the outer lip, with a protruding denticle and the impressed line near the columella. In fact, differences are only shell shape, size, and color detail. The comparatively widely spaced spiral grooves are the most remarkable common feature that also distinguishes the “*punctisulcata*”-group from other species of *Helicinidae* of similar size. The only exception is *H. raresulcata* L. Pfeiffer, 1861, differing in a more globose, slightly

angulated and shouldered shape of the shell (rather similar to *H. merdigera* see under *H. monteverdensis* n. sp.), which furthermore occurs on the Caribbean side of Mexico in Veracruz, whereas the subspecies of the “*punctisulcata*”-group all originate from high altitudes in the Pacific or Central mountains. Besides the types of *H. punctisulcata*, similar spirally grooved specimens come from El Salvador (Laguna de las Ranas, 1,730 m a.s.l., leg. A. Zilch, 16.7.1951, SMF), Guatemala, Huehuetenango Department (5 km W of Aguacatan, 15°20'44"N, 91°23'03"W, 1,910 m a.s.l., leg. F. G. Thompson et al. UF 190472, UF 190225), and Honduras, Santa Barbara Department (Cerro Santa Barbara, ridge above El Cedral, 14°54'55"N, 88°07'30"W, 2,800 m a.s.l., leg. J. Polisar, UF 242644). As can be seen, all these specimens also come from high elevations.

Helicina p. cuericiensis n. subsp. is smaller and has a more intense yellow color. Contrary to *H. p. zunilensis*, the spiral grooves are restricted to the upper half of the whorls. The

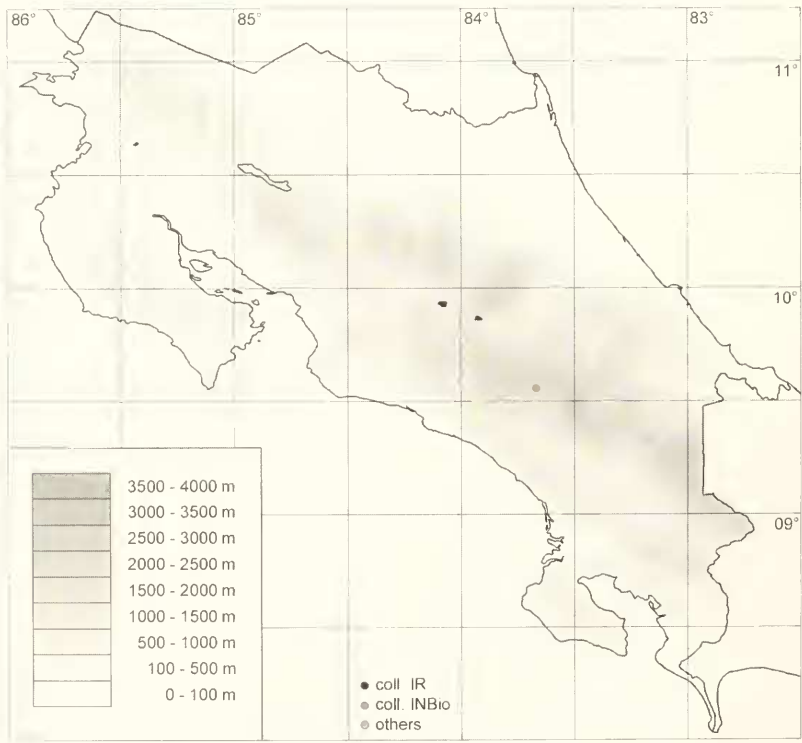


FIG. 97. Records of *Helicina punctisulcata cuericiensis* n. subsp. in Costa Rica.

nominal subspecies appears to be consistently less elevated (broader than high), and the lower margin of the outer lip is less protruding. The few Costa Rican specimens vary remarkably in the relation of height and diameter. But lacking more material for either of the subspecies, the extent of variations, the distribution and ecological data remain only fragmentarily known, which is why the sub-specific classification is maintained, although *H. p. punctisulcata* diverges more strongly from the two southern subspecies. Assuming a restriction to higher altitudes, the three subspecies are separated by the low elevations at the Isthmo de Tehuantepec and the Nicaraguan depression respectively.

An additional single specimen from Costa Rica (San José Province, Parque Nacional Chirripó, Fila Cementerio de la Máquina, 4 km E de San Gerardo, 09°27'49"N, 83°33'40"W, 2,200 m a.s.l., leg. Alexander Alvarado Mendez, 08.10.2001, INBio 3428245) is larger than *H. punctisulcata cuericiensis* n. subsp. and is similar to *H. punctisulcata zunilensis*, but, due to the lack of sufficient material, its proper determination must await further comparative data.

Helicina ("Gemma") *beatrice beatrice*
Angas, 1879

Helicina beatrice Angas, 1879: 484, pl. XL, fig. 13

Helicina beatrice – Pilsbry, 1891: 332

Helicina flavida var. – von Martens, 1890: 39

Helicina beatrice – Fischer & Crosse, 1893: 435

Helicina flavida var. *beatrice* – von Martens,

1900: 606: E-Costa Rica: Talamanca (Pittier);
Valley of Tuis [about 09°51'N, 83°35'W]

(Pittier & Biolley); Santa Clara, 200 m [7.5 km NW of Upala, about 10°56'N, 85°05'W, Alajuela Province] (Biolley); Valley of Alta Coca, near Talamanca, 1,000 m (Pittier) [probably referring to Alto Coén, recently called San José Cabécar, about 09°30'35"N, 83°08'22"W, 500 m a.s.l., Limón Province]; between Uiskur and Mokri [not localized], Alta Talamanca, further in Alta Uren [Alto Urén: 09°23'50"N, 82°59'02"W, 900 m a.s.l., Limón Province], and between Ukatschka and Bruschik, in Alta Taruria [Alto Tararia, about 09°14'30"N, 83°00'30"W, 2,500 m a.s.l. or downstream, Limón Province] (Pittier)

Alcacia (*Leialcacia*) *beatrice* – Wagner, 1908: 83–84, pl. 14, figs. 19–22

Oligyra (*Succincta*) *beatrice beatrice* – Baker, 1922a: 45

Helicina (*Oligyra*) *beatrice* – Pilsbry, 1926a: 59, 69, fig. 3A, 71: Panama: Bocas del Toro: Mono Creek (Olsson)

?*Helicina beatrice* – Pilsbry, 1926b: 127: Costa Rica: La Emilia, < 100 ft. [not localized] (Rehn)

Helicina beatrice – Monge-Nájera, 1997: 113: Costa Rica [in part]

Original Description

"Shell conical, solid, shining; as seen through the lens, very finely transversely striated; whorls 6, very slightly convex, the four uppermost chestnut, the fifth dark red, with an opaque whitish band below the suture, the last pale olive-green, with a similar opaque band at the suture; outer lip thickened, a little expanded and reflexed; aperture quadrately semilunate. Var. Smaller and straw-coloured throughout. Diam. $4\frac{1}{2}$, alt. 5 lin.



FIG. 98. *Helicina beatrice*, lectotype, BMNH 1879.7.22.29, height 10.1 mm; scale bar 2.5 mm.

Very few specimens. "Found only on the hills up to an elevation of 2,500 feet. Animal dark grey above, sides and foot white" (Gabb). Approaches *H. heloisae*, Sallé, but larger and much more conical."

Type Material

BMNH 1879.7.22.29–31 (leg. Gabb)
 Angas (1879: 475) stated that his type material would be placed in the collection of the British Museum, the lot is labeled with "type". Of the three specimens, one represents the dark red opaque whitish banded typical form, the other two the straw colored variety separated by the author. Therefore, the latter two specimens are not regarded as syntypes. The remaining specimen (BMNH 1879.7.22.29), also perfectly matching the figure in the original description, is **here selected as lectotype** of *Helicina beatrix* (Fig. 98). It still bears its operculum and was probably collected live. The two other specimens (one with operculum inside) are much smaller and show a whitish to slightly yellowish color (perhaps faded since the description of Angas), and in one a slight whitish subsutural banding is visible. They are regarded here as *H. beatrix confusa*.

Dimensions:

Lectotype BMNH 1879.7.22.29:

10.1/8.3/8.9/7.7/5.3/7.1/8.2 mm;

BMNH 1879.7.22.30–31 *Helicina beatrix* var. *sensu* Angas, now referred to *H. beatrix confusa*:

7.3/6.9/7.2/6.3/4.3/5.5/5.7 mm

7.0/6.3/6.6/5.9/4.1/5.4/5.6 mm

Type Locality

"Costa Rica, only on the hills up to an elevation of 2,500 feet".

Type Material of Synonymous Taxa or Similar Species

Helicina beatrix nicaraguae (Wagner, 1908)

Alcadia (*Leialcadia*) *beatrix nicaraguae*
 Wagner, 1908: 84, pl. 14, figs. 23–24

Type Material: MIZ 8408: "Nicaragua"

Wagner did not refer to any type material, but his collection contains only one lot with two specimens. It is labeled to be figured and the larger shell perfectly matches the drawing. It is **here selected as lectotype** (Fig. 99). The paralectotype (MIZ 8408b) is not fully grown.

Dimensions:

Lectotype MIZ 8408a:

10.2/8.7/9.1/8.1/5.3/7.3/8.1 mm

Type Locality: Nicaragua

Unfortunately, the locality Nicaragua is not further specified on Wagner's rewritten label, and an original label is lacking, therefore, it cannot be traced further.

Examined Material

LEG. I. RICHLING

Limón: *W Guayacán*, abandoned banana plantation, 10°01'53"N, 83°32'14"W, 520 m



FIG. 99. *Helicina beatrix nicaraguae*, lectotype, MIZ 8408a, height 10.2 mm; scale bar 2.5 mm.

a.s.l., 03.09.1999: (IR 1078); (IR 1081); 12.09.1999: (IR 1087); 15.03.2000: (IR 1360); 17.03.2001: (IR 1606)

INBio COLLECTION

Limón: *Suerre de Jiménez*, 10°11'31"N, 83°44'49"W, 330 m a.s.l., leg. Richard Helling, 26.02.1994: 1 ad. (INBio 1467201) *Reserva Biológica Hitoy Cerere*, Sendero Bobócara, 09°40'53"N, 83°04'09"W, 798 m a.s.l., leg. Alexander Alvarado Mendez, 17.06.1999: 1 ad. (INBio 3542522)

Cartago: (determination uncertain) *?Parque Nacional Barbilla*, bosque secundario, 09°57'52"N, 83°26'59"W, 400 m a.s.l., leg. malacological staff of INBio, 12.01.2001: 1 ad. (INBio 3324279)

?Zona Protectora Río Pacuare, Sector de la Estación de Barbilla, 09°58'50"N, 83°27'08"W, 500 m a.s.l., leg. Alexander Alvarado Mendez, 05.09.2000: 1 s.ad. (INBio 3542905)

Zona Protectora Río Pacuare, Las Brisas de Pacuarito, 10°02'00"N, 83°28'00"W, 400 m a.s.l., leg. malacological staff of INBio, 29.04.2001: 1 ad. (INBio 3418572)

OTHER SOURCES

COSTA RICA

Limón: Finca Los Diamantes, 1,000 ft. [about 10°11'N, 83°37'W], leg. A. Starrett, 22.08.1963: 1 ad. (UF 243509)

Entre Ukatschka et Brushik, Haut Tararia [about 09°14'30"N, 83°00'30"W, 2,500 m a.s.l. or downstream, Limón Province], leg. H. Pittier, IX.98 (ZMB 103251)

San José: Carillo [?about 10°09'N, 83°57'W], coll. E.R. Sykes (BMNH)

Cartago: Turrialba [about 09°54'30"N, 83°41'W], coll. H. Jaeckel: 1 ad. (SMF 209575/1); coll. H. Rolle, coll. C. Bosch: 3 ads., 1 s.ad. (SMF 180668/4); coll. Rolle: 3 ads. (ZMB 103812); Plattino, Turrialba [about 09°54'30"N, 83°41'W], leg. University of Alabama, M. Smith coll. (MS-15183): 4 ads. (UF 95337)

Tuis [about 09°51'N, 83°35'W], leg. H. Pittier: 1 ad. (ZMB 103252)

Costa Rica, without locality further specified: coll. Wagner (MIZ 8407); leg. P. Biolley: 3 ads., 1 s.ad. (MHNN)

Description

Shell (Figs. 100, 336A): Conical-globose, solid, medium sized and shiny. Color: upper whorls chestnut to reddish-brown, getting darker from apex down, towards last whorl changing to pale olive-green-greyish, towards aperture even opaque, in 2.5 last whorls an opaque whitish band directly below suture. Periostracum very thin, shiny and smooth, except for very fine growth lines. Embryonic shell with about 1 whorl; $4\frac{3}{8}$ –5 (lectotype: 5) subsequent whorls very slightly convex; last whorl equally rounded at periphery; upper whorls more rapidly extending in size; whorls rapidly descending, forming a high spire. In the area of the band surface more inflated. Suture slightly impressed. Aperture oblique and in its middle part remarkably curved backwards. Outer lip

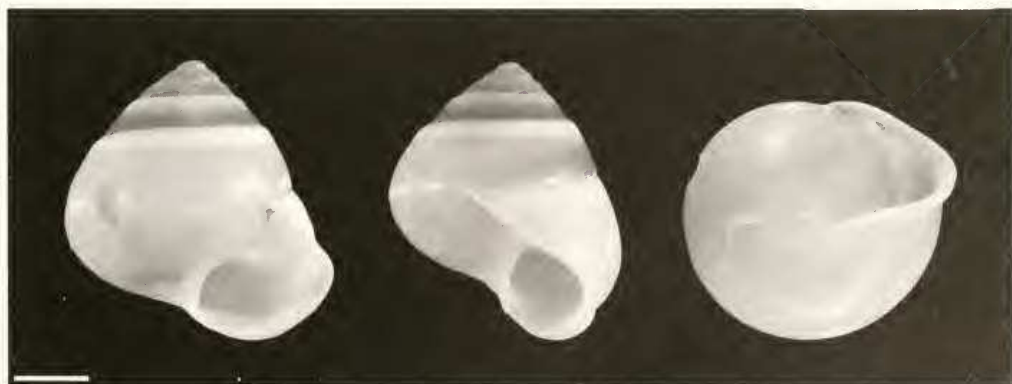


FIG. 100. *Helicina beatrix beatrix*, Guayacán, IR 1087, height 9.4 mm; scale bar 2.5 mm.

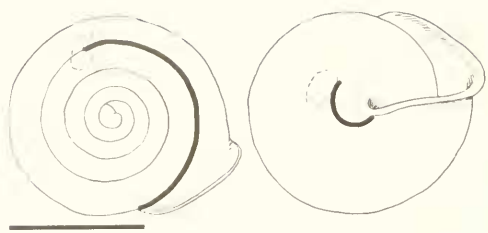


FIG. 101. Axial cleft and muscle attachments of *Helicina beatrix beatrix*, IR 1087; scale bar 5 mm.

always whitish-opaque, similar to the band, thickened and very narrowly reflexed; transition into columella continuous without any notch or only a very small one. Basal callus weakly developed and nearly completely smooth or very little granulated.

Internal Shell Structures: (Fig. 101)

Teleoconch Surface Structure (Fig. 102): The section of the transitional structure encompasses about the first half whorl. A very short zone structured with oblique diverging



FIG. 102. Teleoconch surface structure of *Helicina beatrix beatrix*, 2nd whorl; scale bar 500 μ m.



FIG. 103. Embryonic shell of *Helicina beatrix beatrix*; scale bar 100 μ m.

grooves a replaced by fine growth lines continuing up to the aperture.

Embryonic Shell (Fig. 103): The spirally arranged pits are consistently much smaller than in *Helicina funcki*, and the interspatial distance exceeds the diameter of the pits. The pattern appears much finer, the smooth surface is more prominent.

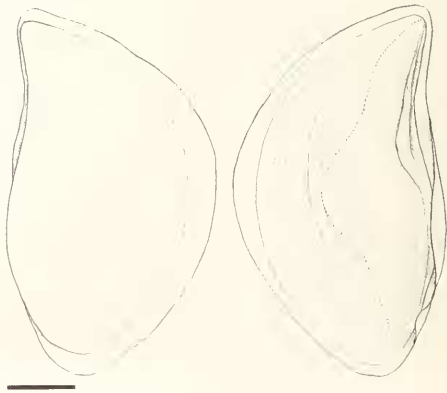


FIG. 104. Operculum of *Helicina beatrix beatrix*, IR 1087; scale bar 1 mm.

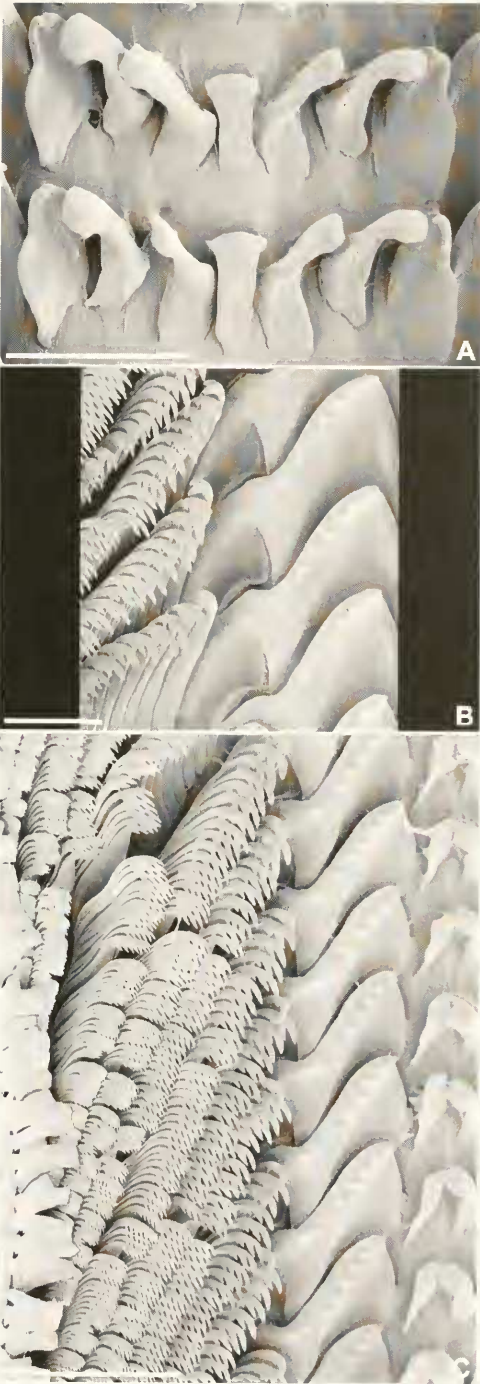


FIG. 105. Radula of *Helicina beatrix beatrix*. A. Centrals. B. Comb-lateral. C. Marginals; scale bars 50 μm (A, B), 100 μm (C).

Diameter: 963 μm (± 33) (900–1010) ($n = 15$) (IR 1078, IR 1081, IR 1087, IR 1360, IR 1606); 1,040 μm (BMNH 1879.7.22.29, lectotype).

Operculum (Fig. 104): Very slightly calcified, calcareous plate covering only part of the outer surface, thickened towards the columellar side. Color horny-amber, only near the columella whitish, but still somewhat transparent. Columellar side slightly S-shaped, both ends acute, upper end pointed, lower slightly rounded.

Animal (Fig. 338A): The soft body is unicolored, whitish yellow throughout, only the tentacles may show a tinge of grey, the mantle is whitish pigmented. There is no trace of any dark spots.

Radula (Fig. 105): Because the radulae of the different subspecies are very similar, they are treated under *Helicina beatrix beatrix*. Central A to C may occasionally bear a few cusps, the B-central most frequently. Comb-lateral with 6–8 denticles, only two aberrant forms with a plain edge or 13 cusps respectively. Cusps on marginals rapidly increasing



FIG. 106. Female reproductive system of *Helicina beatrix beatrix*, IR 1087; scale bar 1 mm.

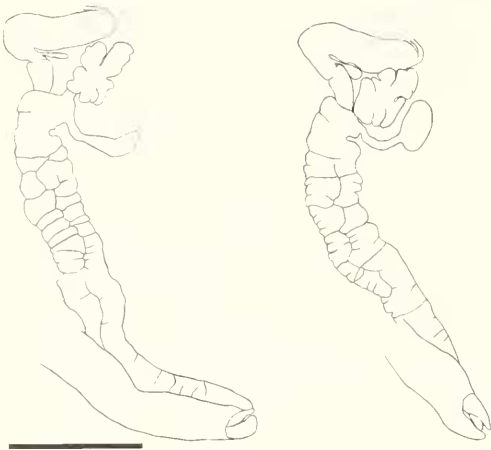


FIG. 107. Variability of the female reproductive system of *Helicina beatriz beatriz*, IR 1087; scale bar 2.5 mm.

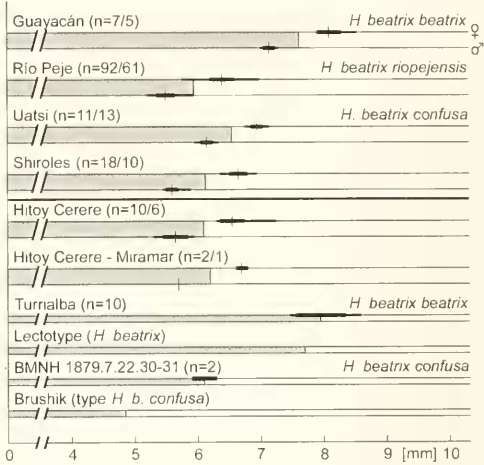


FIG. 109. Minor diameter of shell of different populations of *Helicina beatriz beatriz* and subspecies in Costa Rica according to Table 8; for explanations see Fig. 108.

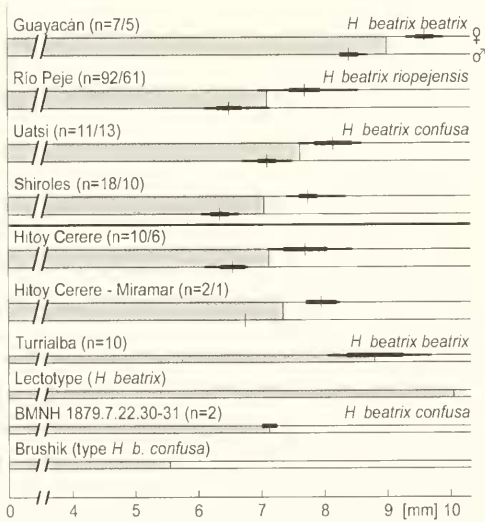


FIG. 108. Shell height of different populations and subspecies of *Helicina beatriz* in Costa Rica according to Table 8; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males or total"; upper line: females, lower line: males if separate; in between and shaded: average of both for comparison with populations of unknown sex; sex of individuals from Hitoy Cerere and Hitoy Cerere - Miramar not determined anatomically (see text).

in number, only in nominal subspecies does a change to more denticles a little more outwards take place, perhaps caused by of the larger size of this form. The same is true for the number of rows of teeth: about 91–138 in *H. b. beatriz*, in the other two subspecies only about 66–79.

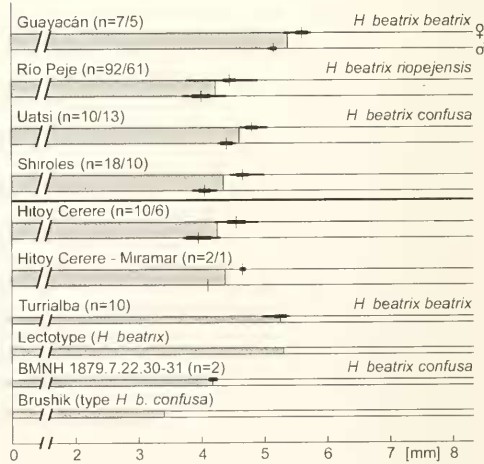


FIG. 110. Expansion of outer lip of different populations and subspecies of *Helicina beatriz* in Costa Rica according to Table 8; for explanations see Fig. 108.

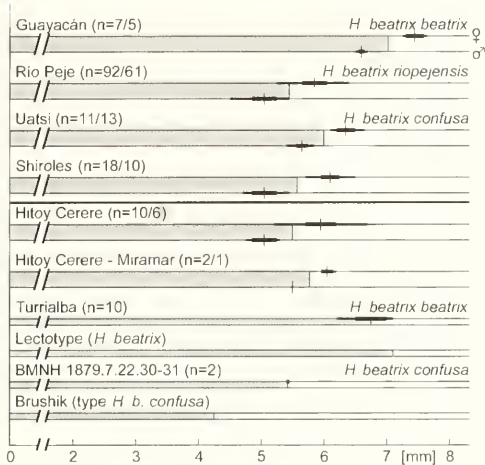


FIG. 111. Height of last whorl of different populations and subspecies of *Helicina beatrix* in Costa Rica according to Table 8; for explanations see Fig. 108.

Female Reproductive System (Figs. 106, 107): The ascending limb of the V-organ is relatively short and stout. The receptaculum seminis is rather large. The bursa copulatrix consists of a few irregularly shaped lobes; the provaginal sac is somewhat inflated and shows a simple outline, the stalk is short. The pallial oviduct is strongly constricted.

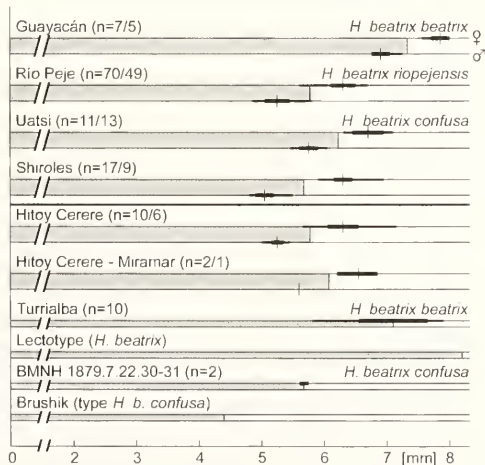


FIG. 112. Height of columellar axis of different populations and subspecies of *Helicina beatrix* in Costa Rica according to Table 8; for explanations see Fig. 108.

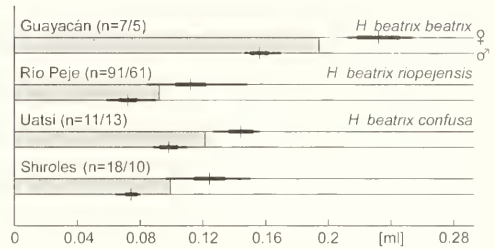


FIG. 113. Shell volume of different populations and subspecies of *Helicina beatrix* in Costa Rica according to Table 8; for explanations see Fig. 108.

Morphometry and Sexual Dimorphism (Table 8, Figs. 108–114)

For comparison, the different subspecies are all discussed in conjunction with the nominal subspecies. The material available for *Helicina beatrix beatrix* remains very scanty, although during the field work several efforts were made to find the species in greater abundance and at different localities. The only specimens studied anatomically are those from Guayacán. Because the “Turrialba” population is united from lots of three different collections, they may originate from different localities around Turrialba.

The specimens of *H. beatrix confusa* included from the INBio collection (Hitoy Cerere, Hitoy Cerere – Miramar) could not be analyzed for their sex by dissection. To make them nevertheless available for morphometric comparison, the degree of sexual dimorphism found in the dissected populations was used to attribute the probable sex to the specimens in reverse conclusion (see below). These data cannot primarily be used to investigate sexual dimorphism.

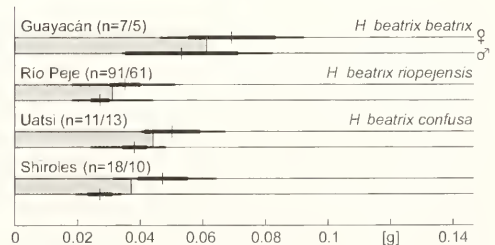


FIG. 114. Shell weight of different populations and subspecies of *Helicina beatrix* in Costa Rica according to Table 8; for explanations see Fig. 108.

TABLE 8. Measurements of different populations and subspecies of *Helicina beatrix* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens; sex of individuals from Hitoy Cerere and Hitoy Cerere – Miramar not determined anatomically (see text) (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

<i>Helicina beatrix beatrix</i> "Guayacán" (altitude 520 m) lots IR 1078, IR 1087, IR 1081							<i>Helicina beatrix riopejensis</i> n. subsp. "Río Peje" (altitude 135 m) lots IR 440, IR 752, IR 1303, IR 1550				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	9.59	0.16	9.31	9.88	7	7.72	0.26	6.95	8.53	92
Height	m	8.39	0.13	8.26	8.71	5	6.51	0.20	6.10	7.17	61
Maj. diam.	f	8.67	0.22	8.33	9.08	7	6.89	0.19	6.00	7.93	92
Maj. diam.	m	7.75	0.08	7.64	7.88	5	5.97	0.15	5.46	6.33	61
Min. diam.	f	8.12	0.21	7.78	8.57	7	6.39	0.18	5.75	7.00	92
Min. diam.	m	7.15	0.10	7.02	7.32	5	5.50	0.14	5.20	5.97	61
Outer lip	f	5.61	0.12	5.31	5.77	7	4.45	0.12	3.75	4.90	92
Outer lip	m	5.13	0.07	5.03	5.22	5	3.98	0.13	3.68	4.40	61
Last whorl	f	7.45	0.13	7.23	7.65	7	5.83	0.18	5.25	6.42	92
Last whorl	m	6.58	0.06	6.49	6.69	5	5.03	0.19	4.53	5.47	61
Col. axis	f	7.83	0.13	7.56	8.01	7	6.28	0.22	5.59	6.88	70
Col. axis	m	6.88	0.15	6.75	7.24	5	5.24	0.19	4.85	5.78	49
Weight	f	0.069	0.014	0.046	0.092	7	0.035	0.005	0.018	0.051	91
Weight	m	0.053	0.018	0.034	0.082	5	0.027	0.003	0.018	0.044	61
Volume	f	0.232	0.014	0.212	0.253	7	0.115	0.009	0.084	0.147	91
Volume	m	0.156	0.006	0.145	0.169	5	0.071	0.005	0.058	0.089	61

<i>Helicina beatrix confusa</i> "Uatsi" (altitude 30 m) lots IR 1112, IR 1113, IR 1567						<i>Helicina beatrix confusa</i> "Shiroles" (altitude 120 m) lots IR 910, IR1327, IR 1594, IR 1600, IR 1646					
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	8.17	0.28	7.59	8.60	11	7.76	0.17	7.40	8.37	18
Height	m	7.10	0.17	6.72	7.50	13	6.35	0.17	6.07	6.67	10
Maj. diam.	f	7.33	0.07	7.20	7.58	11	7.08	0.16	6.77	7.37	18
Maj. diam.	m	6.63	0.16	6.30	6.94	13	6.03	0.13	5.80	6.22	10
Min. diam.	f	6.93	0.10	6.75	7.16	11	6.63	0.17	6.35	6.96	18
Min. diam.	m	6.14	0.11	5.93	6.37	13	5.61	0.12	5.43	5.88	10
Outer lip	f	4.81	0.08	4.61	5.03	10	4.67	0.12	4.47	5.00	18
Outer lip	m	4.42	0.12	4.25	4.63	13	4.04	0.10	3.87	4.25	10
Last whorl	f	6.35	0.16	6.10	6.66	11	6.09	0.14	5.72	6.48	18
Last whorl	m	5.64	0.09	5.42	5.84	13	5.05	0.18	4.72	5.43	10
Col. axis	f	6.68	0.25	6.30	7.08	11	6.32	0.16	5.90	6.96	17
Col. axis	m	5.77	0.15	5.47	6.06	13	5.07	0.17	4.79	5.50	9
Weight	f	0.050	0.009	0.040	0.067	11	0.047	0.008	0.031	0.064	18
Weight	m	0.038	0.004	0.024	0.048	13	0.027	0.004	0.019	0.034	10
Volume	f	0.143	0.007	0.126	0.156	11	0.124	0.010	0.095	0.150	18
Volume	m	0.097	0.006	0.087	0.110	13	0.073	0.004	0.063	0.079	10

(Continues)

(Continued)

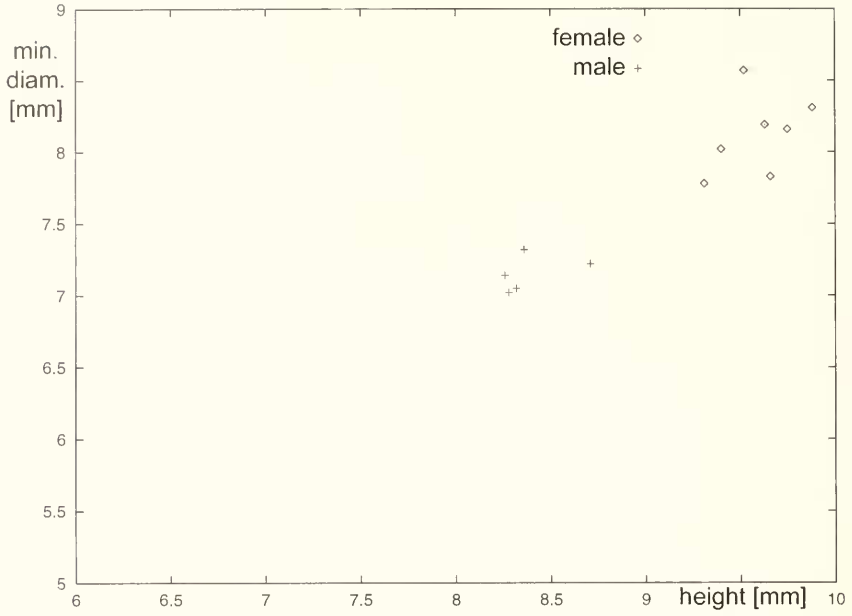
<i>Helicina beatrix confusa</i> "Hitoy Cerere" (altitude 100–798 m) lots INBio 1473618, 1473833, 1473837, 1475069, 1498277, 1543340, 3096421							<i>Helicina beatrix confusa</i> "Hitoy Cerere - Miramar" (altitude 150–300 m) lots INBio 1475230, 1475695, 1476494				
Sex		Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	7.68	0.34	7.09	8.43	10	7.97	0.26	7.71	8.23	2
Height	m	6.56	0.21	6.10	6.78	6	6.73	0.00	6.73	6.73	1
Maj. diam.	f	6.93	0.20	6.47	7.65	10	7.01	0.04	6.96	7.05	2
Maj. diam.	m	6.04	0.25	5.50	6.46	6	6.04	0.00	6.04	6.04	1
Min. diam.	f	6.56	0.18	6.32	7.23	10	6.68	0.08	6.60	6.76	2
Min. diam.	m	5.65	0.18	5.31	5.94	6	5.70	0.00	5.70	5.70	1
Outer lip	f	4.57	0.17	4.22	4.90	10	4.64	0.04	4.60	4.67	2
Outer lip	m	3.96	0.21	3.69	4.30	6	4.09	0.00	4.09	4.09	1
Last whorl	f	5.95	0.23	5.18	6.68	10	6.07	0.11	5.96	6.18	2
Last whorl	m	5.04	0.21	4.74	5.31	6	5.52	0.00	5.52	5.52	1
Col. axis	f	6.30	0.25	5.64	7.17	10	6.54	0.33	6.21	6.86	2
Col. axis	m	5.26	0.12	5.01	5.46	6	5.59	0.00	5.59	5.59	1

<i>Helicina beatrix beatrix</i> "Turrialba" lots SMF 209575/1, SMF 180668/4, UF 95337, ZMB 103812					
	Mean value	Deviation	Min	Max	Number
Height	8.81	0.47	8.06	9.70	10
Maj. diam.	7.96	0.42	7.43	8.62	11
Min. diam.	7.39	0.38	6.68	8.00	11
Outer lip	5.24	0.11	4.94	5.41	9
Last whorl	6.75	0.27	6.19	7.08	10
Col. axis	7.11	0.55	5.82	7.90	7

Morphometry: The typical *Helicina beatrix beatrix* clearly possesses the largest shells among the Costa Rican subspecies of *H. beatrix*. Its shells have a similar size at all three localities. The lectotype is more highly elevated, reflected mainly in height and height of the columellar axis, whereas the specimens from Turrialba have relatively the largest minor diameter. Single specimens of *H. beatrix beatrix* not included in the diagrams fall within the same size range.

The populations of the subspecies *H. beatrix confusa* and *H. beatrix riopejensis* n. subsp. show a very constant pattern of differences between the populations for the different measurements, displaying the same relations of the measurements. The specimens

of Uatsi have the biggest shells. But they all exhibit a smaller size than the nominal subspecies. The relative constancy within the populations and the nearly equal size of the individuals from Shiroles and Hitoy Cerere (Hitoy Cerere – Miramar) suggest a relation to the distribution, because these localities are closer to each other than Uatsi (Fig. 1). Whereas in measurements the two specimens of *H. beatrix* var. *sensu* Angas match the two subspecies well, the lectotype of *H. beatrix confusa* is much smaller. For the subspecies, the lack of material from additional localities still prevents any investigation of a possible correlation of the size to the altitude which could help to relate the small size of the lectotype (from a much



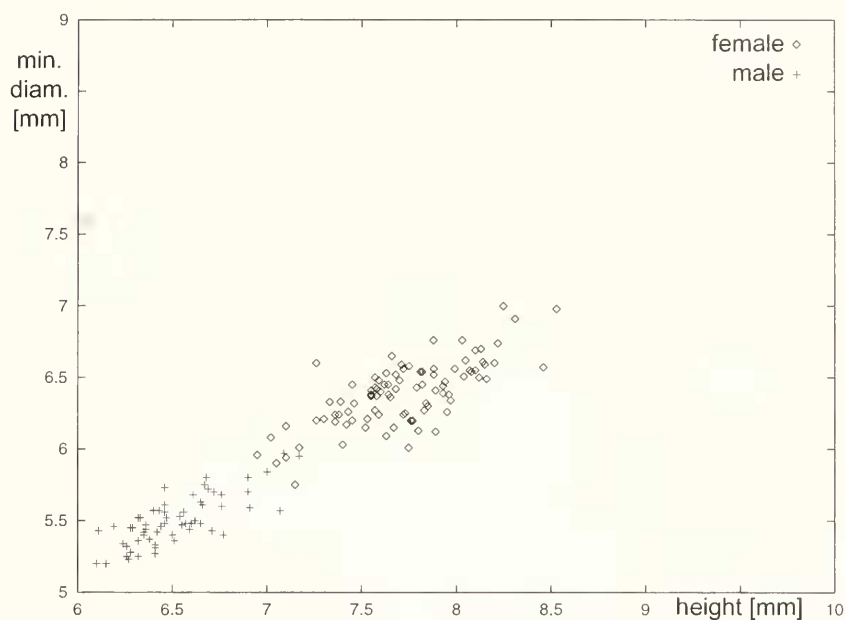


FIG. 117. Range of measurements in females and males of *Helicina beatrix riopejensis* n. subsp. exemplary for height and minor diameter in the population from Río Peje.

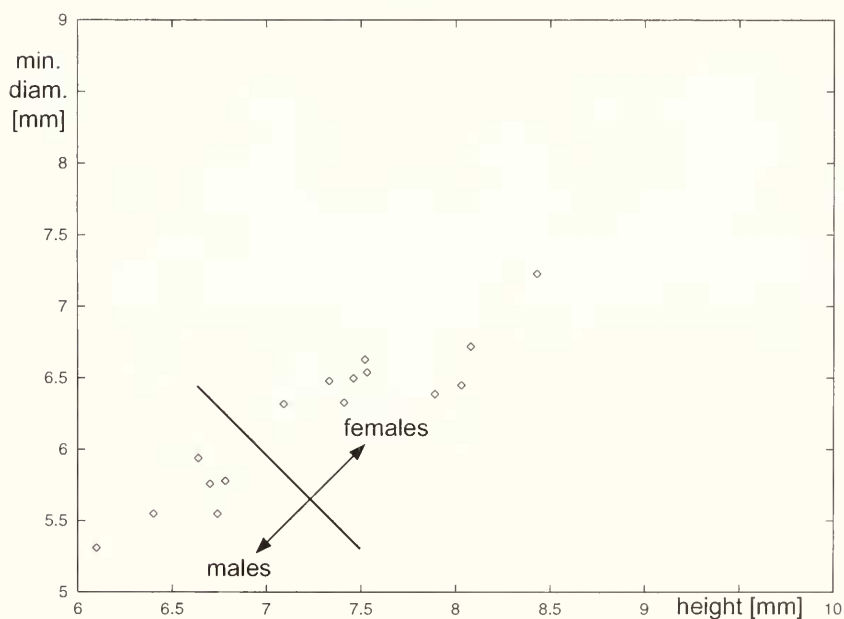


FIG. 118. Plot of measurements for height and minor diameter for individuals of *Helicina beatrix confusa* of unknown sex, exemplary for the population of Hitoy Cerere and the separation proposed.

higher altitude) to the recently collected material. For *H. beatrix beatrix*, the present data do not corroborate a correlation of size with altitude. Within a range from elevations of 330 m (Suerre de Jimenez) to 800–1,000 m (Turrialba) or even up to 2,500? m (Alto Tararia), the size remains nearly constant.

Sexual Dimorphism: All populations and even all measurements show a very clear difference between females and males, in many cases not only within the range of the standard deviation but also for the whole range. This is shown for a population of each subspecies (Figs. 115–117) in data for height and minor diameter, which best separates the sexes. In populations with many individuals (e.g., Río Peje), high extrema are more likely and result in a little overlap. In volume, the males are only about $\frac{2}{3}$ of that (61% to 68%) of females.

The clear difference between both sexes can be used to plot measurements (e.g., minor diameter to height) of specimens of unknown sex (Fig. 118, Hitoy Cerere) in order to attribute them to their most likely sex. But the differences between the populations also demonstrate that this method will only work for specimens from one and the same locality, and the lot from "Turrialba" could not be separated (Fig. 119) because it does not represent a single population.

The differences of the specimens of *H. beatrix* var. *sensu* Angas to the lectotype of *H. beatrix* are out of the range of sexual dimorphism, supporting their exclusion from typical *H. beatrix*.

Habitat

Helicina beatrix beatrix was found by the author at only one locality at Guayacán. There it inhabits a small abandoned banana field on a steep hillside surrounded by secondary growth and partly swampy meadows for cattle. Specimens were aestivating or on the underside of green banana leaves or crawling in curled, dried leaves. Originally the area was covered by rain forest, and it seems to be a relic occurrence of the species. All negative records and the few specimens in collections suggest that *H. beatrix beatrix* is a rare subspecies.

Distribution (Fig. 120)

Although records are scarce, the occurrence shows a remarkable pattern. As already ob-

served by Gabb and cited in the original description, the species is said to occur only on hills up to an elevation of 2,500 feet. In fact *Helicina beatrix* inhabits the Caribbean mountain slopes of the Cordillera Central and the Cordillera de Talamanca. The localities can be attributed to the slopes of three regions: the valley between the volcanoes Barva and Irazú/Turrialba, the Caribbean side of the Valle Central along the Río Reventazón between the Volcán Irazú and northern Cordillera de Talamanca, and the Valle de Talamanca. The verified range of altitude is from about 330 m to 1,000 m or even up to 2,500 m depending on the exact location of "Alto Tararia". The most northern record from Santa Clara near the frontier to Nicaragua is uncertain.

Discussion

Helicina beatrix beatrix is understood as the large whitish-opaque form with reddish-brown upper whorls. The determination of two of the three lots from the Barbilla/Río Pacuare area (INBio 3324279, INBio 3542905) is uncertain; the size of the adult specimen is similar to the nominal subspecies; the color approaches that of *H. b. confusa*. A common feature of *H. beatrix beatrix* and the other subspecies is the general shape as described above and the subsutural opaque band. Furthermore, the outer lip is typically strongly curved backwards, especially in females. Against the background that intermediate forms of the subspecies are lacking and a sympatrical occurrence implying a specific separation is uncertain, the status of subspecies is tentatively maintained or suggested for the population from Río Peje. But certain hints for a sympatrical existence of *H. beatrix beatrix* and *H. b. confusa* have to be mentioned. The type locality of *H. beatrix confusa* (Brushik, Alto Tararia) is probably close to "between Ukatschka and Brushik, Alto Tararia" recorded for *H. beatrix beatrix*, although the exact location is uncertain (see below). Furthermore, a recently collected lot in the collection of INBio from the Sendero [= trail] Bobócara in the reserve Hitoy Cerere contains both subspecies, and the very top of the mountain Cerro Bobócara is given as locality, but is most likely not the source of all specimens. In the extremely mountainous and steep terrain, a short distance of the trail probably already encompasses different habitats at different altitudes. Therefore, the data do not contribute to an assessment of the status of *H. beatrix* and subspecies.

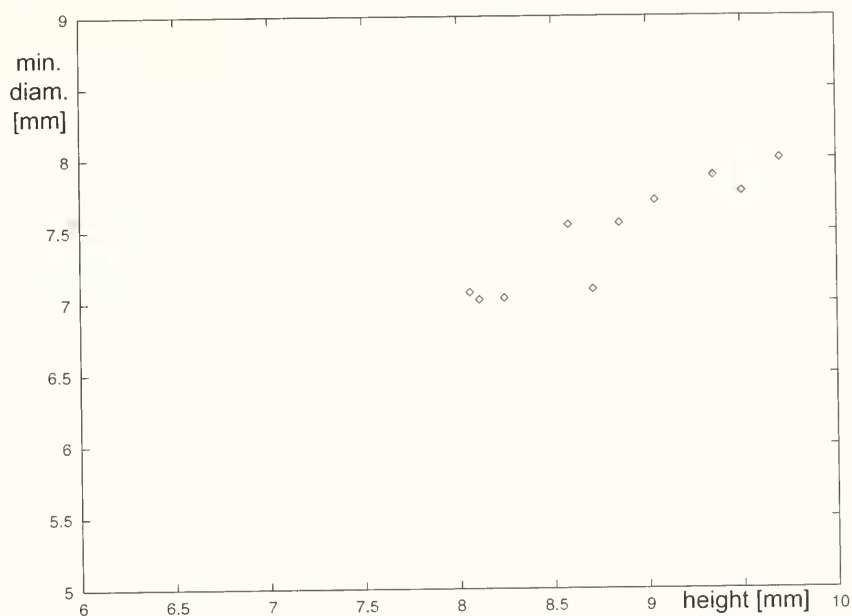


FIG. 119. Plot of measurements for height and minor diameter for individuals of *Helicina beatrix beatrix* of unknown sex, exemplary for the specimens from "Turrialba" (probably not single populations) for which a separation is not possible.

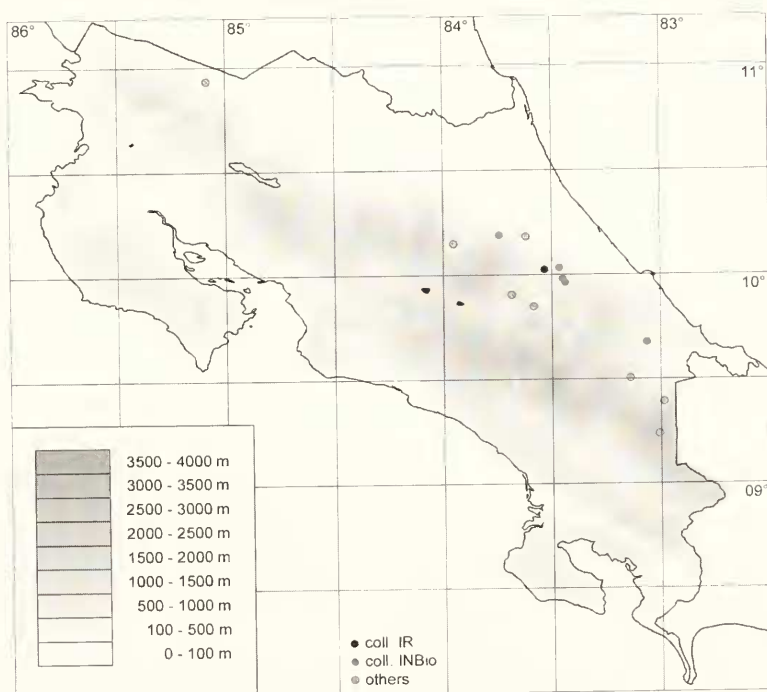


FIG. 120. Records of *Helicina beatrix beatrix* in Costa Rica.

The type lot of *H. beatrix* is of unknown origin and most likely it is also composed of specimens from different localities, because the smaller two belong to a different subspecies. The knowledge of well-localized records of *H. beatrix* is very limited, but among those, the lot ZMB 103251 from high up in the mountains from the Valle de Talamanca (southern Caribbean side) most closely resembles the lectotype in having a high, elevated shell. According to recent and previous findings, populations at Guayacán, Turrialba and Tuis are characterized by more globular shells, thus suggesting that the lectotype probably was not collected in the area of the Río Reventazón and its tributaries between Turrialba and Siquirres, which was comparatively easily accessible at the end of the 19th century as the most direct connection between San José and Puerto Limón on the Caribbean.

The record from Santa Clara remains doubtful, because it is far out of the verified distribution and the original material has not been found. A confusion with *H. gemma* which occurs in this region, can be excluded for three reasons: (1) Biolley (1897) and von Martens (1900) also reported this species for the area as *H. oweniana anozona* and von Martens (1900) as *H. oweniana coccinostoma*, (2) von Martens (1900) characterized the specimens as no less than 10 mm in diameter and 9 in height, whereas *H. gemma* displays a remarkably constant size of about 5 to 7 mm in height, and (3) the orange outer lip of *H. gemma* would rather suggest an identification as *H. oweniana* than *H. beatrix*, exactly as von Martens obviously treated *H. gemma* in his publication. Except for the doubtful record of *H. beatrix nicaraguae*, the species has not been reported from the adjacent Nicaragua. In the face of absence of the original material and the limited knowledge on Nicaraguan Helicinidae, it still remains doubtful.

In *Helicina beatrix nicaraguae*, the whorls very evenly increase in size, forming a regular spire, which is less inflated than in *H. beatrix beatrix*. The whorls are more convex, therefore the suture is more deeply impressed. The whitish band under the suture is less distinct and more slender. The basic color is yellowish, with a tendency to greenish, towards the aperture lighter and changing to opaque.

On account of the poorly investigated Nicaraguan terrestrial molluscan fauna, it is impossible to render any judgement about the possible origin or distribution. According to the

Costa Rican records, *H. beatrix* and subspecies are confined to the southern Caribbean slope and coastal plain with its most northern record verified at about Guápiles (10°13'N), or with uncertainty near the Nicaraguan border at Santa Clara. The only record for Nicaragua is that of Wagner (1908) of his new subspecies. Supposing that the record from Santa Clara is attributed to another species and considering that *H. beatrix* and subspecies seem to be absent from the very lowlands, that is, the southern Nicaragua, there appears to be a gap in the distribution towards Nicaragua. Otherwise, specimens from Isla Colón (Isla Colon, Las Gratas, 5 km NNW of Bocas del Toro, 09°23'25"N, 82°16'15"W, 70 m a.s.l., leg. F.G. Thompson (FGT-4724), 17.09.1990: 2 ads. (UF 167532); interior of Colon Island, leg. McGinty coll., 28.03.1953: 1 s.ad. (UF 185607) (Fig. 121), Bocas del Toro Province, Panama, adjacent to the Costa Rica distribution, show a surprising similarity in shape and color. With a height of 9.6 mm, the largest shell nearly reaches the size of the lectotype. An investigation of the Nicaraguan malacofauna would be required to prove whether the type locality of *H. beatrix nicaraguae* is in this country, or whether the lectotype in fact came from Panama.

Von Martens (1890–1901) misinterpreted *H. beatrix* as a variety of *H. flavida* because he had not seen original specimens. Subsequent authors (Pilsbry, 1891; Fischer & Crosse, 1893) stressed the distinctness of *H. beatrix*, and von Martens agreed with this in his supplement.



FIG. 121. *Helicina beatrix nicaraguae*, Panama, Isla de Colón, UF 167532, height 8.9 mm; scale bar 2.5 mm.

Pilsbry (1926a) twice mentions *H. beatrix* from Bocas del Toro Province, Panama: specimens agreeing in size with the nominal subspecies from a certain locality and additional individuals not further specified in their origin that are remarkably smaller, thus resembling *H. beatrix confusa* in size. Furthermore, the identification and localization of the Costa Rican record by Pilsbry (1926b) remains doubtful, because altitudes of less than 100 feet would be exceptional for the nominal subspecies.

Helicina ("Gemma") *beatrix confusa*
(Wagner, 1908)

Helicina beatrix var. – Angas, 1879: 484, pl. XL, fig. 13 [non *Helicina beatrix* Angas, 1879]

Alcadia (*Leialcadia*) *beatrix confusa* Wagner, 1908: 84, pl. 14, fig. 25

Oligyra (*Succincta*) *beatrix confusa* – Baker, 1922a: 45

Helicina beatrix – Monge-Nájera, 1997: 113: Costa Rica [in part] [non Angas, 1879]

Original Description

"Gehäuse viel kleiner [als *Alcadia beatrix*], dünnschaliger, gelbgrün mit rötlichem Gewinde; das niedrigere, konvexe Gewinde besteht nur aus $4\frac{1}{2}$ deutlicher gewölbten Umgängen, der letzte ist unten weniger abgeflacht.



FIG. 122. *Helicina beatrix confusa*, lectotype, MIZ 8409, height 5.6 mm; scale bar 2.5 mm.

D = 7.3, H = 7.2

Deckel wie bei der typischen Form.

Fundort: Costa Rica."

Type Material

MIZ 8409: "Brusik [sic] Ht. Tararia"

Wagner did not refer to any type material, but his collection contains only one specimen he singled out as type material. It is labeled "to be depicted" and agrees very well with the illustration. The specimen is therefore **here selected as lectotype** (Fig. 122).

Dimensions:

Lectotype: 5.6/5.3/5.7/4.9/3.4/4.2/4.4 mm

Type Locality

"Costa Rica" (figure caption erroneously Nicaragua); restricted by the type selection to Brushik, Alto Tararia [about 09°14'30"N, 83°00'30"W, 2,500 m a.s.l. or downstream, Limón Province]

Unfortunately, Wagner used to rewrite most of the labels and only occasionally retained the original, thereby not always preserving all information (Riedel, 2000). In the present case, it can be referred to "Brushik, Haut Tararia" [Spanish: Alto Tararia], a source also named by von Martens (1900) for material collected by Pittier. At that time, Pittier was the only one intensively studying the region of the Valle de Talamanca and its adjacent mountain slopes. Despite an intensive search for the locality, it is difficult to rediscover it. It is known that Pittier maintained good relations with the indigenous Cabécar and Bribrí, which inhabit the Valle de Talamanca and settle along the four main rivers – Río Telire, Río Coén, Río Lari and Río Urén – and their tributaries high up in the mountains. Throughout this region, neither Brushik nor Alto Tararia or related names could be found on detailed maps. Much further south a Cerro Tararia ["cerro" = "mountain", 09°09'03"N, 82°58'27"W, 2,690 m a.s.l.] exists, which most likely is not the locality mentioned, because it forms a part of the very central mountain chain and lacks any access route. Furthermore, "Alto" followed by a name of a river usually refers to a main settlement along the river in the mountains, for example, Río Lari – Alto Lari. Therefore, Alto Tararia may mean the upper part of the Río Tararia [about 09°14'30"N, 83°00'30"W, 2,500 m a.s.l. or downstream], which really exists southeast of Cerro Kamuk. Again, it is difficult

to gain access to the region, settlements or trails are not shown on maps. From Valle de Talamanca, it means following the river Río Lari or Río Urén to their headwaters and to cross the Cerro Kamuk to reach the high region of Río Tararia draining towards Panama. Because other Pittier localities are very reliable, this appears to be the best interpretation, because the material also may have been given to Pittier by indigenous people and probably not all indigenous names and trails were incorporated in maps, and some may even have been forgotten or lost.

Examined Material

LEG. I. RICHLING

Limón: Southern road from *Bribri* to *Shiroles*, small banana plantation near creek, 09°35'17"N, 82°52'46"W, 50 m a.s.l., 15.03.1997: (IR 170)

W Bribri, road to *Uatsi*, about 09°38'11"N, 82°51'48"W, 30 m a.s.l.: abandoned field with *Heliconiaceae* and *Eucalyptus*: 17.03.1997: (IR 182); 12.03.1999: (IR 765); 15.09.1999: (IR 1112); (IR 1113); 15.03.2001: (IR 1567); wooded valley within banana plantation, 50 m a.s.l.: 15.03.2001: (IR 1585)

N Shiroles: along *Quebrada Kirio*, 09°35'38"N, 82°57'20"W: 120 m a.s.l.: 15.03.1997: (IR 161); 100 m a.s.l.: 12.03.1999: (IR 764); 09.08.1999: (IR 910); 06.03.2000: (IR 1327); (IR 1329); 16.03.2001: (IR 1594); (IR 1646); *Cerro Mirador*, along trail, 09°36'37"N, 82°57'43"W, 430 m a.s.l.: 16.03.2001: (IR 1600)

INBIO COLLECTION

Limón: *Parque Nacional La Amistad*, *Quebrada Cachabri* (toma de agua), 09°29'29"N, 82°59'37"W, 360 m a.s.l., leg. Gerardina Gallardo, 26.11.1996: 1 ad. (INBio 1488199)

Reserva Biológica Hitoy Cerere: Sendero Toma de Agua, 09°40'31"N, 83°01'36"W, 100 m a.s.l.: 20.04.1994: 5 ads. (INBio 1473837); 1 ad. (INBio 1473618); 2 ads., 1 juv. (INBio 1473833); 13.08.1994: 3 ads., 2 s.ads., 13 juvs. (INBio 1475069) (all leg. Zaidett Barrientos); *Sendero Toma de Agua*, 09°40'22"N, 83°01'35"W, 160 m a.s.l.: leg. Marianella Segura, 14.07.1994: 1 s.ad. (INBio 1478208); 1 juv. (INBio 1478209); *Sector Miramar, Hitoy Cerere*, 09°37'50"N, 83°00'52"W, 300 m a.s.l.: 13.06.1994: 1 ad. (INBio 1476494); 04.07.1994: 1 ad. (INBio 1475695) (all leg. Gerardo Carballo); *Sector Miramar*, 09°38'03"N, 83°00'45"W, 300 m a.s.l.: leg. Zaidett Barrientos, 08.10.1994: 1 ad. (INBio 1475716); *Sendero a Captación de Agua*, 09°39'59"N, 83°01'31"W, 200 m a.s.l.: leg. Alexander Alvarado Mendez, 28.04.1999: 3 ads., 2 s.ads. (INBio 1498277); *Sendero Tepezcintle*, 09°40'18"N, 83°01'43"W, 140 m a.s.l.: leg. Alexander Alvarado Mendez, 28.04.1999: 1 s.ad. (INBio 1496288); *Sendero Bobócara*, 09°40'53"N, 83°04'09"W, 798 m a.s.l.: leg. Alexander Alvarado Mendez, 17.06.1999: 1 ad., 1 s.ad. (INBio 1543340)

Reserva Indígena Talamanca, Sector Amubri, 09°30'53"N, 82°57'19"W, 70 m a.s.l.: leg. Gerardina Gallardo, 14.06.1994: 1 ad. (INBio 1477505); 1 ad. (INBio 1477553);

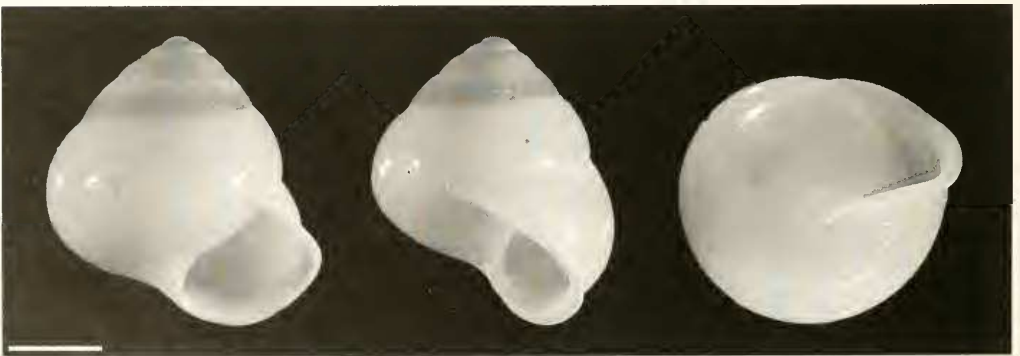


FIG. 123. *Helicina beatrix confusa*, Shiroles, IR 910, height 7.8 mm; scale bar 2.5 mm.

Sector Miramar, Senderos a Río Moín, 09°37'44"N, 83°00'32"W, 150 m a.s.l.: leg. Zaidett Barrientos, 08.11.1994: 1 ad., 1 s.ad., 3 juvs. (INBio 1475230)

Reserva Indígena Tayni, Sendero Tepezcuintle, 09°40'22"N, 83°01'46"W, 180 m a.s.l., leg. Alexander Alvarado Mendez, 22.04.1999: 1 ad. (INBio 3096421)

OTHER SOURCES

COSTA RICA

Limón: N of Río Moín [Valle de Talamanca!], 572 000 E, 397 600 S [09°37'45"N, 83°00'38"W], 220 m a.s.l., leg. E.L. Raiser (ELR-086), 11.08.1994: 1 ad., 2 s.ads. (UF 41440)

Costa Rica, without locality further specified: leg. Gabb: 2 spec. (BMNH 1879.7.22.30–31)

Description

Shell (Figs. 123, 336B, C): Conical-globose, rather thin, small sized, shiny. Color: upper whorls yellowish-red, horny changing continuously to yellow at the beginning of body whorl and getting nearly white towards aperture. The opaque whitish band directly below suture very slender. Shell surface shiny and smooth, except very fine growth lines. Embryonic shell with about 1 whorl; 4–5 (lectotype: $3\frac{3}{4}$) subsequent whorls very slightly convex; last whorl equally rounded at the periphery; upper whorls slightly more rapidly extending in size; whorls regularly descending, forming a nearly blunt spire. Suture slightly impressed. Aperture oblique and in its middle part remarkably curved backwards. Outer lip whitish-opaque similar to the band, slightly thickened and very narrowly reflexed; transition into columella con-

tinuous without a very little notch. Basal callus weakly developed and nearly completely smooth or very little granulated, umbilical area whitish.



FIG. 125. Teleoconch surface structure of *Helicina beatrix confusa*. A. Changes in the apical part. B. 2nd whorl; scale bars 500 µm (A), 100 µm (B).

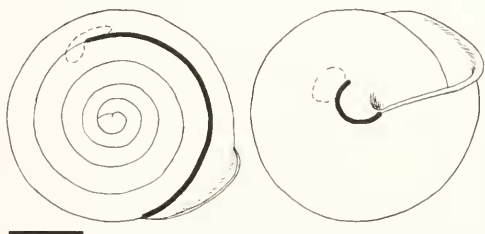


FIG. 124. Axial cleft and muscle attachments of *Helicina beatrix confusa*, IR 1113; scale bar 2.5 mm.

Internal Shell Structures: (Fig. 124)

Teleoconch Surface Structure (Fig. 125): Similar to *Helicina b. beatrix*, but the relation between the transitional structure and the pattern of oblique diverging grooves is reversed, the former nearly disappearing.

Embryonic Shell (Fig. 126): Among the specimens investigated, the spiral lines are less numerous than in the nominal subspecies. Otherwise, the embryonic shell structure is similar. The diameter is smaller.

Diameter: 889 μm (± 32) (800–950) ($n = 21$) (IR 1113, IR 1567); 840 μm (MIZ 8409, lectotype); 900 μm ($n = 2$) (BMNH 1879.7.22.30–31, *Helicina beatrix confusa*).

Operculum (Fig. 127): Very slightly calcified, calcareous plate covering only part of the outer surface. Color horny-amber, only near the columella whitish, but still somewhat transparent. Columellar side slightly S-shaped, both ends acute, upper end pointed, lower slightly rounded.

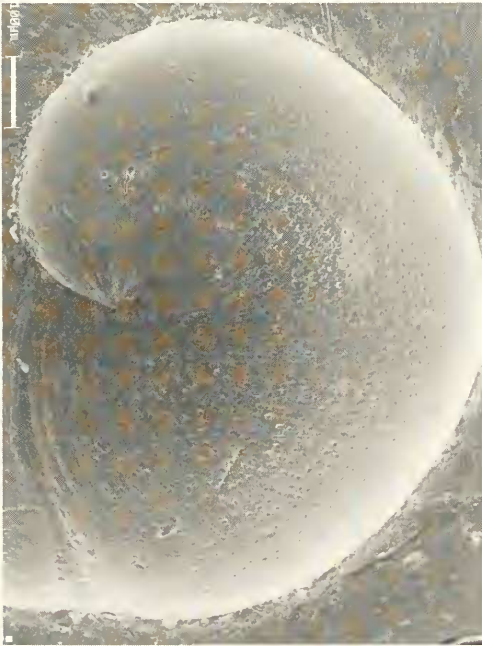


FIG. 126. Embryonic shell of *Helicina beatrix confusa*; scale bar 100 μm .

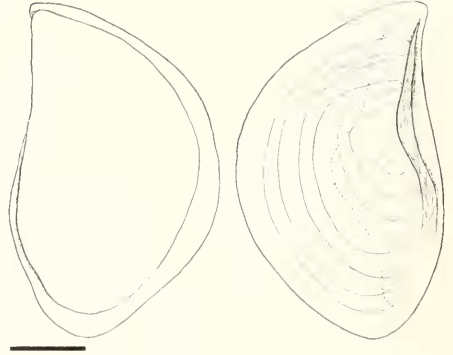


FIG. 127. Operculum of *Helicina beatrix confusa*, IR 1113; scale bar 1 mm.

Animal (Figs. 337F, G): The body color is similar to *Helicina beatrix beatrix*, especially within the yellow-shelled population from Uatsi. In some specimens from Shiroles (more frequently in individuals with orange-brownish tinged shells), the dorsal part of the head region including eyes and tentacles and the foot is more or less grey-blackish and the mantle is greyish pigmented as well.

Radula: See *Helicina beatrix beatrix*.

Female Reproductive System (Figs. 128, 129): The structures are similar to the nominal subspecies; the bursa copulatrix bears even fewer lobes.



FIG. 128. Female reproductive system of *Helicina beatrix confusa*, IR 1113; scale bar 1 mm.



FIG. 129. Variability of the female reproductive system of *Helicina beatrix confusa*, IR 1113; scale bar 2.5 mm.

Morphometry and Sexual Dimorphism

See *Helicina beatrix beatrix*.

Habitat

The population "Uatsi" inhabits an apparently abandoned agricultural area surrounded

by small banana fields. The vegetation consists mainly of Heliconiaceae and some bamboo (Poaceae). *Helicina beatrix confusa* was found on the underside of the leaves of Heliconiaceae and occasionally on *Monstera* spec. (Araceae) climbing the few big trees left of the previous forest. By way of contrast, the main site at Shiroles is a small creek in what seemed to be primary forest. Snails were crawling and aestivating on the leaves of various small-leaved plants of the undergrowth along the creek. Two specimens were discovered in the leaf litter. Additionally specimens were found on leaves of lower branches of big trees within the forest. Near Shiroles, *H. beatrix confusa* lives sympatrically with *H. funcki* and *H. escondida* n. sp.

Distribution (Fig. 130)

Helicina beatrix confusa is confined to the southern Caribbean mountain slopes of the northern Cordillera de Talamanca and adjacent hilly areas, namely in the Valle de Talamanca and Valle de Estrella. Like the other subspecies, it seems to be absent near the coast. A more northern occurrence is questionable, a record from the Río Pacuare-

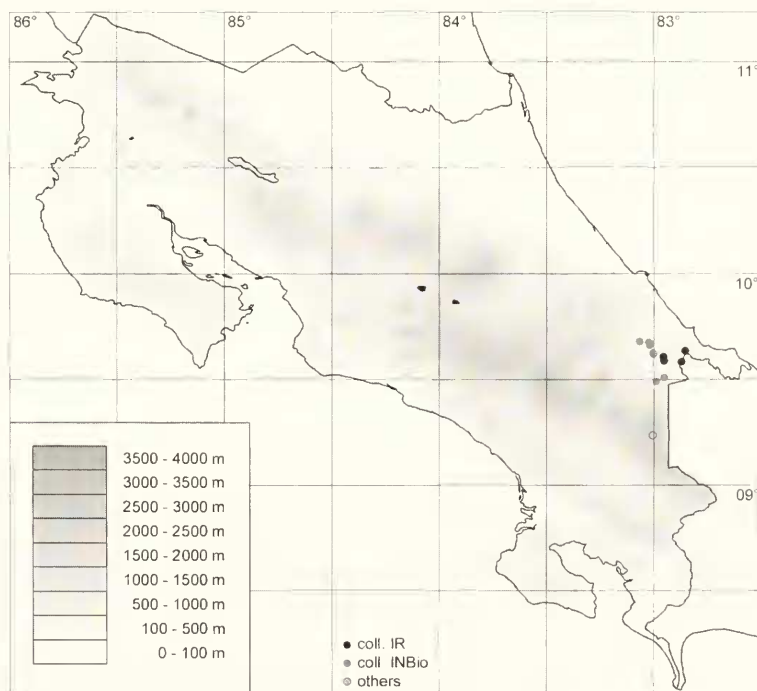


FIG. 130. Records of *Helicina beatrix confusa* in Costa Rica.

Barbilla area at altitudes of 400 to 500 m has tentatively been attributed to the nominal subspecies. The foothills of the Talamanca have otherwise only been poorly investigated, not only because they are difficult to access, but also because the very local and patchy distribution renders the snails difficult to find. There is evidence for a more northerly absence, at least at lower altitudes, because several less elevated sites at Río Siquirres, Río Pacuarito, Río Barbilla, near the road between Siquirres and Limón, were checked with negative results although other Helicinidae at other places inhabiting the same habitats – *H. funcki*, *H. escondida* n. sp., *H. chiquitica*, *H. gemma* – were found.

Discussion

The description given above applies to the lectotype. The specimen is adult, but the outer lip is still not fully developed. The less elevated shell renders is likely to be a male, although it cannot be concluded with certainty due to the lack of comparative material from the same locality. If this assumption is correct,

the average size of *Helicina beatrix confusa* would be bigger than indicated by the lectotype. Nevertheless, all specimens studied are clearly bigger. But because the specimens morphometrically studied originate from lower altitudes of sites not far from each other, although comparatively far away from the type locality at presumably higher altitudes, and the shape and the mode of color is similar, they are attributed to this subspecies. The lectotype looks like a reduced form. The distribution within the Valle de Talamanca and adjacent slopes additionally supports this classification.

In the specimens recently collected, the whitish band is like in the nominal subspecies broader, but occasionally it can also be as slender as in the lectotype. The color of the whorls varies within the populations and among them, but the outer lip and umbilical area are constantly whitish-opaque. The individuals from Uatsi possess shells with brownish whorls at the apex that during growth change more or less quickly to a pale or more often bright yellow color above the periphery. At least the beginning of the last whorl is yellow



FIGS. 131, 132. *Helicina beatrix riopejensis* n. subsp., Río Peje. FIG. 131. Holotype, INBio 3542625, height 7.8 mm. FIG. 132. Paratype 1, INBio 3542626, height 6.6 mm; scale bar 2.5 mm.

below the subsutural whitish band. Towards the aperture the color fades to pale yellowish-whitish. Specimens from Shiroles may display a similar color, but in many the brownish-reddish-orange of the upper whorls does not change up to the aperture. Similarly the color becomes lighter below the periphery. In general, the yellow form seems to be more frequent.

***Helicina* ("Gemma") *beatrice riopejensis*
Richling, n. subsp.**

Type Material

Holotype: INBio 3542625, female (leg. I. Richling, 09.03.1999, ex IR 752)

Paratype 1: INBio 3542626, male (same data as holotype)

Paratype 2: ZMB 103882, female (same data as holotype)

Paratype 3: ZMB 103883, male (same data as holotype)

Dimensions:

Holotype: 7.8/7.0/7.4/6.5/5.9/4.6/6.4 mm

Paratype 1: 6.6/6.0/6.5/5.6/5.0/4.1/5.3 mm

Paratype 2: 8.1/6.8/7.3/6.5/6.1/4.6/6.7 mm

Paratype 3: 6.3/5.9/6.5/5.5/5.2/4.1/5.1 mm

Type Locality

SE-Costa Rica, Limón Province, SW of Liverpool (about 24 km W of Puerto Limón) along Río Peje, 09°55'46"N, 83°13'15"W, 135 m a.s.l.

Etymology

The subspecies is named after its origin, the Río Peje.

Examined Material

LEG. I. RICHLING

Limón: SW Liverpool: Río Peje and small tributary, 09°56'35"N, 83°14'01"W, 110 m a.s.l.: 12.03.1997: (IR 125); along Río Peje, bordering forest with palms, 09°55'46"N, 83°13'15"W, 135 m a.s.l.: 04.03.1998: (IR 440); 09.03.1999: (IR 752); 03.03.2000: (IR 1303); (IR 1305); (IR 1306); 13.03.2001: (IR 1550)

Description

Shell (Figs. 131, 132, 336D): Conical-globose, rather solid, medium sized, shiny. Color: up-

per whorls light yellowish-horny-amber, becoming darker from apex down, especially in the course of the last whorl changing to bright orange. A small but very distinct opaque whitish band directly below the suture, color of whorl most intensive towards the band. Shell surface shiny and smooth, only structured with very fine growth lines. Embryonic shell with about 1 whorl; $4\frac{3}{8}$ ($3\frac{3}{4}$ – $4\frac{1}{2}$) subsequent whorls very slightly convex; last whorl equally rounded at the periphery; upper whorls slightly more rapidly extending in size; whorls rapidly descending, forming a high spire. Suture slightly impressed. Aperture oblique and remarkably curved backwards, last whorl regularly descending and inserting exactly at periphery. Outer lip always bright orange in continuation of last whorl, thickened and very narrowly reflexed; transition into columella continuous with a little notch. Basal callus very weakly developed and nearly completely smooth or very little granulated.

Internal Shell Structures: (Fig. 133)

Teleoconch Surface Structure (Fig. 134): Similar to *Helicina b. beatrice*, but the zone of oblique diverging grooves is more pronounced.

Embryonic Shell (Fig. 135): The structure is similar to that of *Helicina beatrice confusa*. Figure 135B shows a common phenomenon also seen in other species: a few spiral lines of pits become indistinguishable.

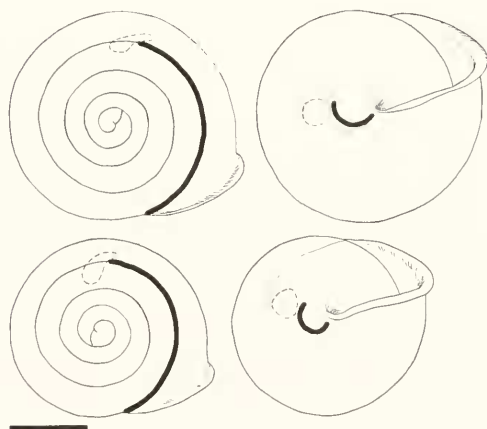


FIG. 133. Axial cleft and muscle attachments of *Helicina beatrice riopejensis* n. subsp., INBio 3542625, 3542626; scale bar 2.5 mm.

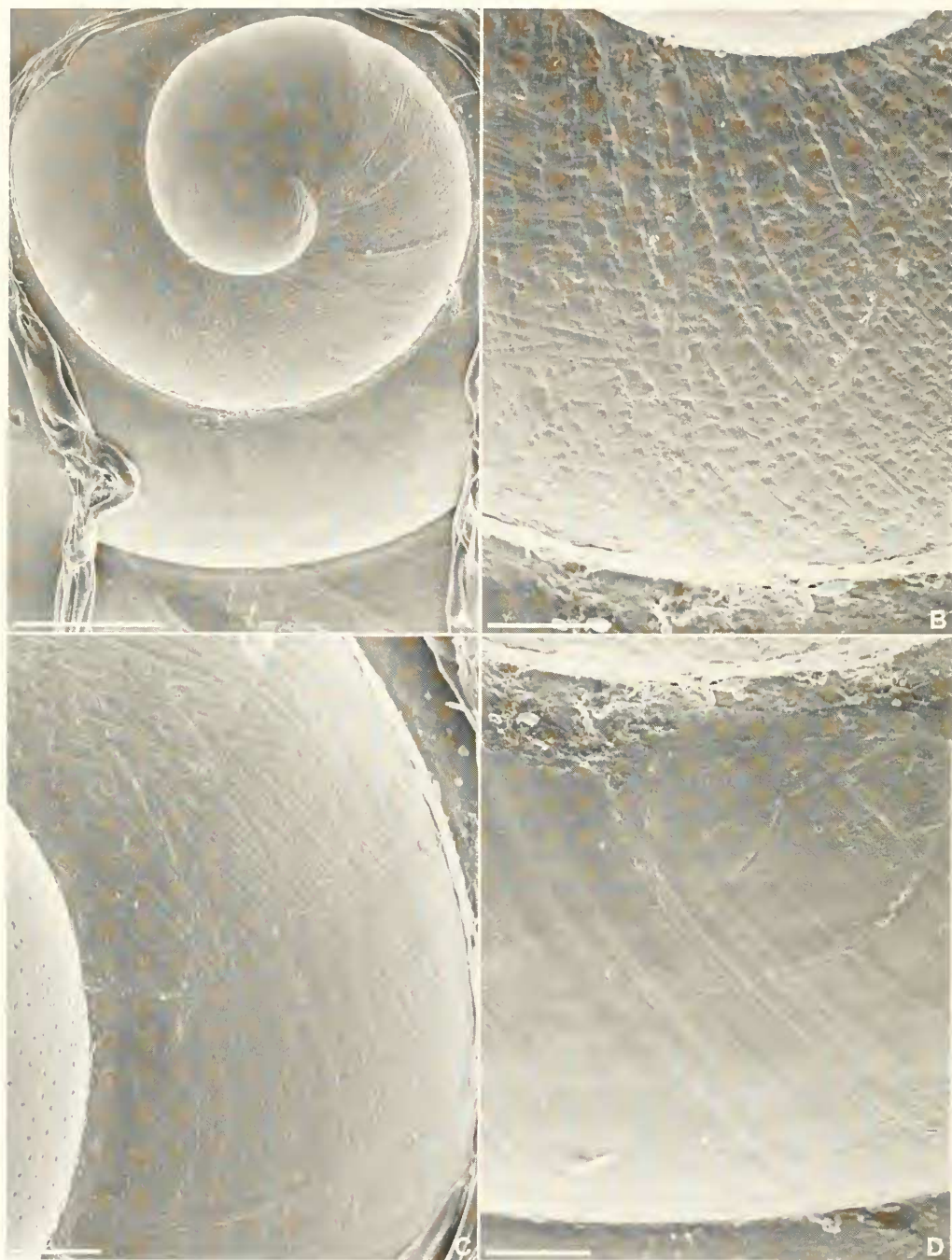


FIG. 134. Teleoconch surface structure of *Helicina beatrix riopejensis* n. subsp. A. Embryonic shell to 2nd whorl. B. 1st whorl, zone of transitional pattern and begin of transformation to next structure. C. 1st whorl, pattern of oblique diverging grooves. D. 2nd whorl, smooth surface with growth lines; scale bars 500 μ m (A), 100 μ m (B-D).

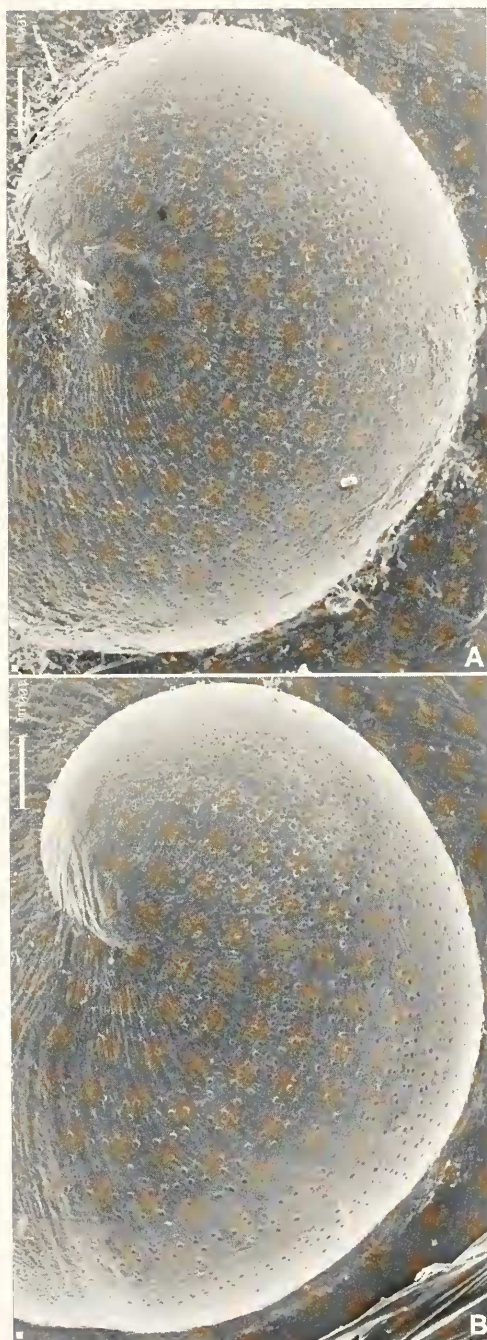


FIG. 135. Embryonic shell of *Helicina beatrix riopejensis* n. subsp.; scale bar 100 μ m.



FIG. 136. Operculum of *Helicina beatrix riopejensis* n. subsp., INBio 3542625; scale bar 1 mm.

Diameter: 878 μ m (\pm 31) (800–940) (n = 22) (IR 1303, IR 1550).

Operculum (Fig. 136): Very slightly calcified, calcareous plate covering only part of the outer surface, thickened towards the columellar side. Color orange to dark red, only at columellar side and in the area of the nucleus yellowish-transparent. Columellar side slightly S-shaped, both ends acute, upper end pointed, lower slightly rounded.

Animal (Fig. 337H): As with other subspecies, *Helicina beatrix riopejensis* n. subsp. lacks any spotted pattern on the mantle. But the dorsal and upper lateral sides of head and a median stripe on the posterior foot are black. Only on the middle of the head there is a lighter area. The tentacles are black as well. A greyish-blackish mantle pigmentation gives the semitransparent shell a greenish-brownish appearance, making the white band even more prominent.

Radula: See *Helicina beatrix beatrix*.

Female Reproductive System (Figs. 137, 138): The structures are similar to the nominal subspecies, except for the bursa copulatrix, which is more regularly and deeply lobed; the receptaculum seminis appears consistently smaller.

Morphometry and Sexual Dimorphism

See *Helicina beatrix beatrix*.

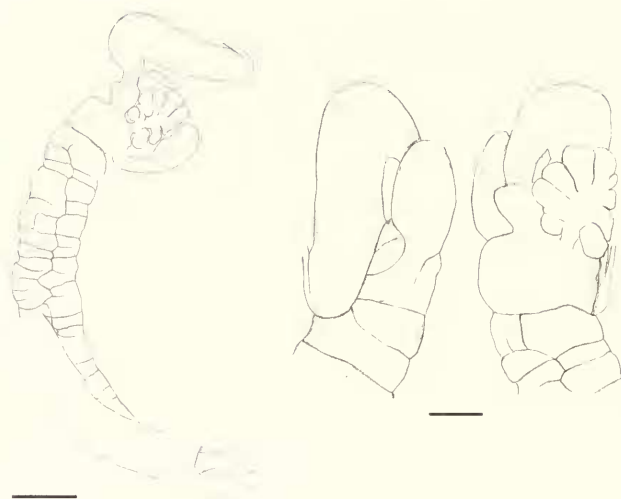


FIG. 137. Female reproductive system of *Helicina beatrix riopejensis* n. subsp., apical complex in natural position, dorsal and ventral view, IR 752; scale bars 1 mm (left), 0.5 mm (right).

Habitat

At the type locality, this subspecies is relatively abundant. The undergrowth of the vegetation of the banks of the creek is mainly composed of Heliconiaceae, different palm species, and Araceae. During wet weather, *Helicina beatrix riopejensis* n. subsp. was found crawling nearly everywhere on the leaves with no obvious preference for any particular plants. A higher abundance on leaves of palms and Heli-

coniaceae may have resulted from the much larger surface of the leaves and the easier search. When aestivating, the specimens were found mainly on the underside of the leaves close to the middle rib. On palms, individuals were observed up to about 5–6 m above the ground. Along the Río Peje, the subspecies lives sympatrically with *H. funcki*, but it was not discovered at several other localities in the area along Río Victoria, Río Blanco, Río René or Río Quito, where *H. funcki* also occurs.

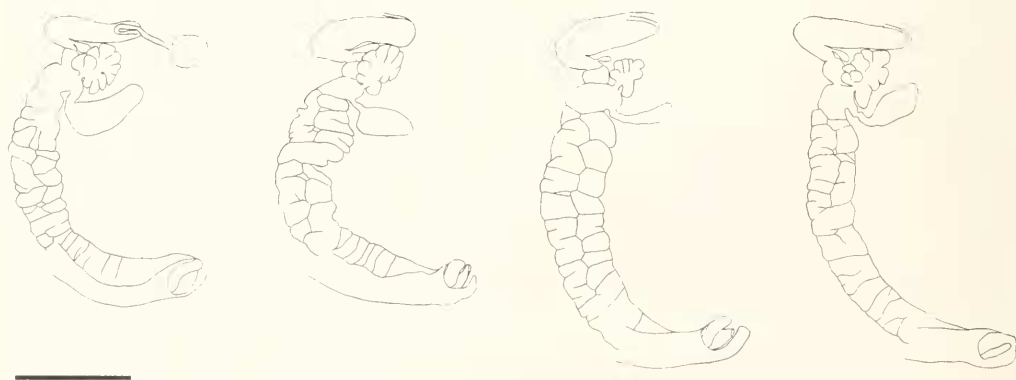


FIG. 138. Variability of the female reproductive system of *Helicina beatrix riopejensis* n. subsp., IR 752; scale bar 2.5 mm.

Distribution (Fig. 139)

Up until now, the subspecies has only been found along the upper part of the Río Peje and a few small tributaries around the type locality. The site belongs to the hilly Caribbean lowlands close to the northeastern foothills of the Cordillera de Talamanca.

Discussion

Few specimens exhibit a dark red spot at the apex. The tinge of orange towards the aperture may be paler or even bright red. Otherwise, the color is very constant within the population investigated.

Helicina beatrix riopejensis n. subsp. differs from the nominal species and other subspecies in the color of the outer lip, which in the other subspecies is consistently whitish, independently of the varying color of the whorls. Furthermore, in *H. beatrix beatrix*, *H. b. confusa*, and *H. b. nicaraguae* the color of the whorls becomes lighter towards the aperture (normally whitish at least in the umbilical

area), whereas in *H. b. riopejensis* n. subsp. it turns darker, even in the umbilical area. In general, the whitish band is more slender in *H. b. riopejensis* n. subsp.

With respect to the orange outer lip, the subspecies closely resembles *H. gemma*, but the latter consistently lacks the distinct whitish band under the suture. Its suture seems somewhat more strongly impressed, and the whorls appear to be more convex. Whereas *H. beatrix beatrix* is very clearly distinguished from *H. gemma*, *H. beatrix riopejensis* n. subsp. seems to represent a somewhat intermediate form showing several similarities to both species. Besides the aspects of the shell color, the length of the axial cleft equals the conditions of *H. gemma* and deviates from the other subspecies of *H. beatrix*. On the other hand, *H. beatrix riopejensis* n. subsp. completely lacks the spotted mantle pigmentation of *H. gemma* and, with respect to the morphometry, it would clearly represent the population with the largest specimens. According to all investigated populations of *H. gemma*, the species is much more constant in size than

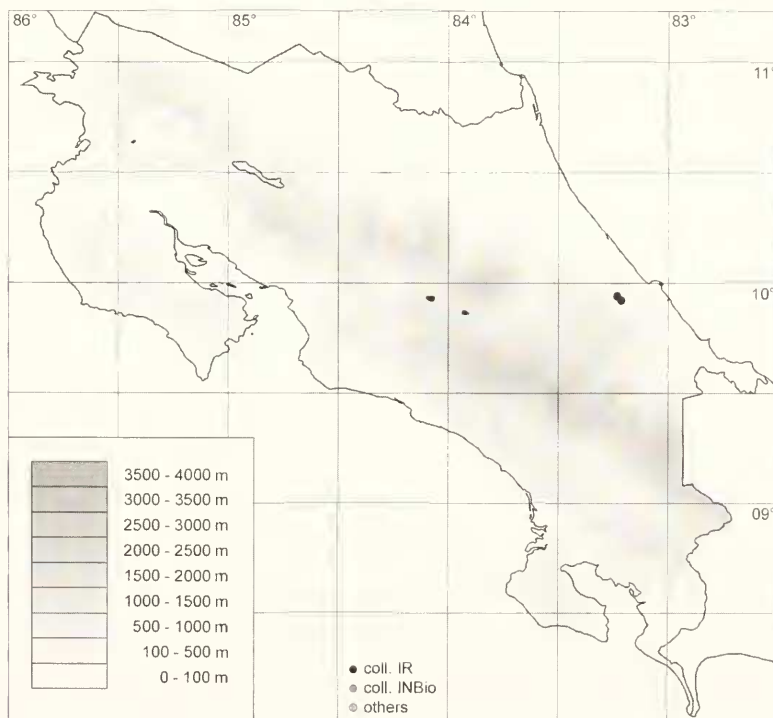


FIG. 139. Records of *Helicina beatrix riopejensis* n. subsp. in Costa Rica.

the other species. At the same locality at the Río Peje, it reaches its largest sizes, but in Tortuguero, where *H. gemma* occurs sympatrically, the population has a smaller shell size than *H. beatrix riopejensis* n. subsp., making a comparison with the conditions of other species contradictory. With the present state of knowledge, "*riopejensis*" is tentatively referred to *H. beatrix*, but further data may reveal closer affinities to *H. gemma*. Nevertheless, the differences between "*riopejensis*" and both species justify a recognition at subspecific level.

Helicina ("*Gemma*") *talamancensis*
(Richling, 2001)

Helicina oweniana – Monge-Nájera, 1997: 113:
Costa Rica [in part] [non L. Pfeiffer, 1849]
Helicina beatrix – Monge-Nájera, 1997: 113:
Costa Rica [in part] [non Angas, 1879]
Oligyra talamancensis Richling, 2001: 3–5
(text figure)

Original Description

See "Description".

Type Material

Holotype: INBio 3404978, female (leg. I. Richling, 24.3.1997) (Fig. 140)
Paratype 1: INBio 1494509, female
(Puntarenas, 3 km NE de la Escuela de Llano Bonito, 08°44'54"N, 83°02'04"W, 920 m a.s.l., leg. Socorro Avila, 24.03.1997)
Paratype 2: INBio 3389580 (same data as paratype 1)
Paratype 3: ZMB 103368, male (same data as holotype)

Paratype 4: ZMB 103385, probably female, empty shell (from type locality, leg. I. Richling, 29.8.1999)

Paratypes 5–12: INBio 1494642: 7 adults, 1 juvenile (same data as paratype 1)

Paratypes 13–14: INBio 1487761: 2 juveniles (Puntarenas, 3.5 km de la Escuela de Llano Bonito Carretera a San Vito, 08°44'37"N, 83°02'04"W, 840 m a.s.l., leg. Socorro Avila, 24.03.1997)

Dimensions (height/greatest diameter):

Holotype: 9.2/9.2 mm

Paratype 1: 9.1/8.7 mm

Paratype 2: 9.2/8.8 mm

Paratype 3: 8.2/8.3 mm

Type Locality

SW-Costa Rica, Puntarenas Province, Fila Costeña, north of Bajo Bonito (locally called Llano Bonito), north of Río Claro, 8°44'41"N, 83°02'09"W, 980 m a.s.l., probably primary rain forest bordered by secondary growth.

Type Material of Synonymous Taxa or Similar Species

Helicina terryae Rehder, 1940

Helicina terryae Rehder, 1940: 350, fig. 16

Type Material: USNM 536026 (not USNM 539026 as given in Rehder, 1940): holotype (Fig. 141)

Dimensions (given in original description, height/greatest diameter):

Holotype: 8.2/9.8 mm

Type Locality: Panama, Chiriquí Province.

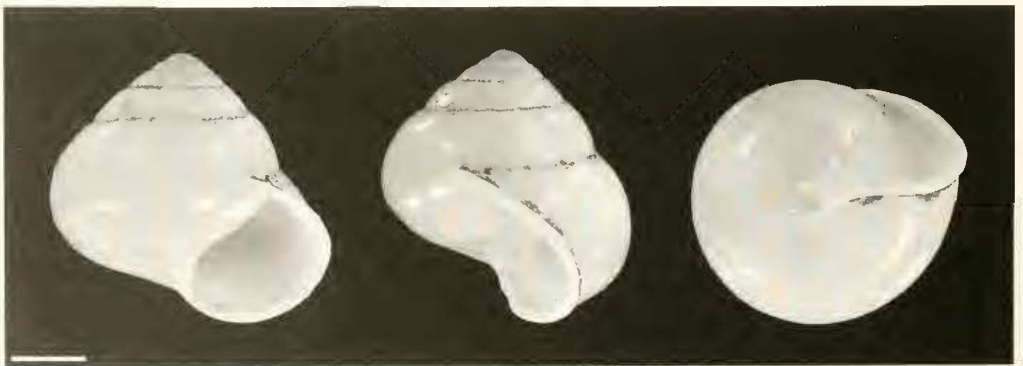


FIG. 140. *Helicina talamancensis*, holotype, INBio 3404978, height 9.2 mm; scale bar 2.5 mm.

Examined Material

LEG. I. RICHLING

Puntarenas: S *San Vito*, forest opposite the Wilson Botanical Garden, Las Cruces, 08°46'57"N, 82°57'40"W, 1,160 m a.s.l., 29.08.1999: (IR 1018)

N *Neily*, road from Ciudad Neily to San Vito, open area with a few trees, 08°40'23"N, 82°56'44"W, 180 m a.s.l., N *Neily*, 23.03.1997: (IR 210)

Fila Costeña, north of *Bajo Bonito* (locally called Llano Bonito), N of Río Claro, rain forest, 08°44'41"N, 83°02'09"W, 980 m a.s.l., 24.03.1997: (IR 222); 15.02.1999: (IR 580); 29.08.1999: (IR 1029), (IR 1661); (IR 1030); 06.03.2001: (IR 1487); (IR 1489)

Refugio Nacional de Fauna Silvestre Gofito, rain forest, 08°39'26"N, 83°10'50"W, 100 m a.s.l., 14.02.1999: (IR 567); 10.02.2000: (IR 1166)

INBIO COLLECTION

San José: San Isidro, Area de Conservación la Amistad, *Parque Nacional Chirripó*, Estación Santa Elena, Finca del Gringo, 09°23'31"N, 83°35'42"W, 1,300 m a.s.l.: leg. A. M. Maroto, 29.09.1995: 1 ad. (INBio 3542536)

Puntarenas: *Reserva Forestal Golfo Dulce*: Cerro de Oro, 08°33'46"N, 83°29'24"W, 150 m a.s.l.: leg. Eida Fletes, 30.10.1995: 1 ad. (INBio 1498769), 1 ad. (INBio 1498766); Cerro de Oro, Quebrada Terranosa, 08°34'11"N, 83°30'15"W, 140 m a.s.l.: leg. Ronald Villalobos, 05.10.1995: 1 ad. (INBio 1485176); Rancho Quemado, 08°40'35"N, 83°34'33"W, 250 m a.s.l.: leg. Zaidett Barrientos, 18.03.1994: 1 juv. (INBio 1475394)

Playa Blanca, 08°38'18"N, 83°26'16"W, 0 m a.s.l., leg. Guillermo Mena, 04.09.1995: 1 juv. (INBio 1479918)

Fila Cal: 24 km de San Vito hacia Ciudad Neilly, 08°41'36"N, 82°56'36"W, 780 m a.s.l.: 14.01.1995: leg. Luis Angulo, 2 ads., 1 juv. (INBio 1480714); leg. Angela Mora Maroto: 2 ads. (INBio 1481246); leg. Socorro Avila: 4 ads., 2 juvs. (INBio 1481353); leg. Marcos Moraga: 1 ad., 1 juv. (INBio 1481564); leg. Alejandro Azofeifa: 1 ad. (INBio 1482605); leg. Francisco Alvarado: 3 s.ads. (INBio 1495690); 29.08.1995: leg. Marianella Segura, 3 ads., 2 s.ads. (INBio 3121201); 740 m a.s.l.: leg. Ronald Villalobos: 4 juvs. (INBio 1481514); 24.5 km S en la carretera de San Vito hacia Ciudad Neilly, 08°40'55"N, 82°56'23"W, 600 m a.s.l.: leg. Zaidett Barrientos, 21.11.1995: 4 ads., 1 juv. (INBio 1485120); leg. A. Picado, 21.11.1995: 2 ads., 2 s.ads., 1 juv. (INBio 3542530); leg. M. Segura, 21.11.1995: 2 ad., 1 s.ad. (INBio 3542545)

4.5 km NW de Ciudad Neily, Camino Paralelo al Río Caño Seco, Colectado en hojarasca en helechos, 08°40'50"N, 82°57'25"W, 180 m a.s.l.: leg. M. Chinchilla, 22.11.1995: 4 ads., 1 s.ad. (INBio 3542526) *Jardín Botánico Wilson*, Sendero a Río Jaba, 08°47'13"N, 82°58'04"W, 1,160 m a.s.l., leg. Zaidett Barrientos, 10.03.1995: 1 ad. (INBio 1485093)

Estación Pittier: 09°01'32"N, 82°57'46"W, 1,660 m a.s.l.: leg. Angela Mora Maroto, 15.01.1995: 1 ad., 2 juvs. (INBio 1481397); Sendero Pittier, 09°01'11"N, 82°57'54"W, 1,540 m a.s.l.: leg. malacological staff of INBio, 06.11.1995: 4 ads., 1 juv. (INBio 1488141); Sendero Río Gemelo, 09°01'36"N,



FIG. 141. *Helicina terryae*, holotype, USNM 536026, height 8.2 mm; scale bar 2.5 mm (photograph: R. Hershler).

82°57'26"W, 1,640 m a.s.l.: leg. Annia Picado, 13.01.1995: 1 juv. (INBio 1481168) *Parque Nacional La Amistad, Coto Brus*, sendero a Cerro Pittier, 600 m NW de la Estación, 09°01'44"N, 82°57'54"W, 1,750 m a.s.l., leg. Marcos Moraga, 06.11.1995: 1 ad. (INBio 1484619)

Parque Nacional La Amistad, Estación Pittier, Sendero a Cerro Pittier: 09°02'05"N, 82°57'39"W, 1,800 m a.s.l.: leg. Luis Angulo, 06.10.1995: 1 juv. (INBio 1485495); 09°01'43"N, 82°57'54"W, 1,750 m a.s.l.: leg. M. Moraga, 19.06.1996: 1 ad. (INBio 3542538); *Sendero a Altamira, 900 m NW de la estación*, 09°01'52"N, 82°58'05"W, 1,760 m a.s.l.: leg. Evelio Alfaro, 15.01.1995: 1 ad. (INBio 1480719), 1 ad. (INBio 1480725); leg. Angela Mora Maroto: 2 ads. (INBio 1481219), 1 ad. (INBio 1481236); 1 ad. (INBio 3542544); *Sendero a Río Canasta*, 09°01'51"N, 82°58'05"W, 1,740 m a.s.l.: leg. M. Moraga, 14.06.1996: 1 ad. (INBio 3542540)

Parque Nacional La Amistad, Estación Altamira, Sendero a Estación Biolley: 09°01'59"N, 83°00'39"W, 1,340 m a.s.l.: leg. Marianella Segura, 13.10.1994: 1 ad. (INBio 1485516); 09°01'47"N, 83°01'07"W, 1,300 m a.s.l.: leg. Alexander Alvarado Mendez, 10.09.2001: 1 ad. (INBio 3394313)

Parque Nacional La Amistad, Cerro Biolley, 09°02'25"N, 83°00'39"W, 1766 m a.s.l., leg. Roberto Delgado, 17.06.1994: 1 ad. (INBio 1467066)

Parque Nacional La Amistad, Cabagra, Puesto Altamira, Sendero a Cerro Biolley, 09°02'12"N, 83°00'39"W, 1,600 m a.s.l., 13.06.2001: 1 s.ad. (INBio 3318186); 3 ads. (INBio 3318194) (all leg. Alexander Alvarado Mendez)

Puntarenas, *Parque Nacional La Amistad, Pittier*, Puesto Altamira, sendero Casa Coca,

09°02'25"N, 82°59'24"W, 1,800 m a.s.l., leg. Alexander Alvarado Mendez, 12.05.2001: 1 ad., 1 s.ad. (INBio 3317088)

OTHER SOURCES

COSTA RICA

San José: determination uncertain? 4.3 mi SW of San Isidro del General on Road to Dominical [about 09°20'N, 83°44'W], 01.08.1971: 2 ads. (UF 69848)

Puntarenas: Rincón [about 08°42'30"N, 83°29'30"W], R. Casebeer, 28.06.1963: 1 ad. (UF 243510)

Etymology

The species is named after the southern central mountain chain in Costa Rica, the Cordillera de Talamanca, which forms the greatest remaining undisturbed area of primary forest in the country.

Description

Shell (Figs. 140, 336E): conical-globose, rather solid, medium sized, shiny. Color: yellowish to

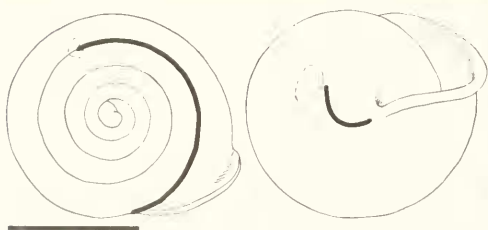


FIG. 142. Axial cleft and muscle attachments of *Helicina talamancensis*, IR 1030; scale bar 5 mm.



FIG. 143. Teleoconch surface structure of *Helicina talamancensis*, 2nd whorl; scale bar 100 μ m.

whitish-opaque (holotype); in some specimens the last whorl yellowish-white and the upper whorls with a more or less strong tendency to a pale orangish-red color. Periostracum very thin, shiny and smooth, except very fine growth lines. Embryonic shell with about 1 whorl; $4\frac{1}{8}$ – $4\frac{3}{4}$ subsequent whorls slightly convex; last whorl equally rounded at periphery; upper whorls more rapidly extending in size, so that shell (especially the female's) appears somewhat rounded and less pointed in apical part. Suture slightly impressed. Aperture oblique and in its middle part remarkably curved backwards. Outer lip always whitish, thickened, very narrowly reflexed, appearing somewhat rounded at edge; transition into columella continuous, with a slight notch. Basal callus weakly developed and nearly completely smooth or very little granulated.

Internal Shell Structures: (Fig. 142)

Teleoconch Surface Structure (Fig. 143): The transitional pattern covers only about $\frac{1}{4}$ of a whorl; the structure is weakly developed. The smooth zone with just the fine growth lines follows directly.

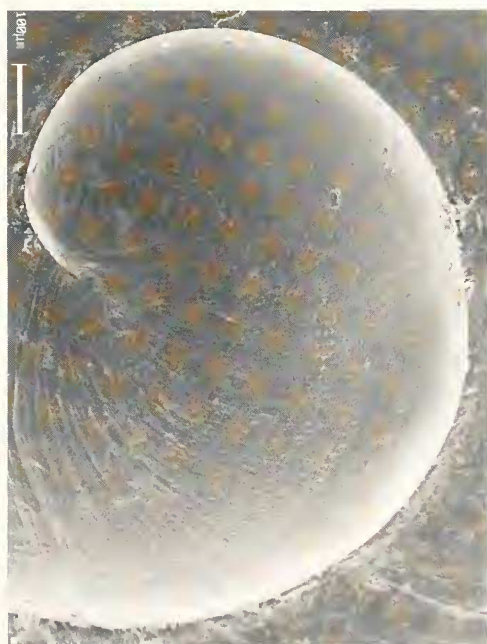


FIG. 144. Embryonic shell of *Helicina talamancensis*; scale bar 100 μ m.

Embryonic Shell (Fig. 144): In comparison with *Helicina beatrix*, the pitted pattern is even less prominent in *H. talamancensis*. The embryonic shell appears nearly smooth. Diameter: 933 μ m (\pm 40) (840–1,000) (n = 18) (IR 222, IR 1028, IR 1030).

Operculum (Fig. 145): Very slightly calcified, calcareous plate covering only part of the outer surface. Color horny-amber, only near the columella whitish, but still somewhat transparent. Columellar side S-shaped, both ends acute, upper end pointed.

Animal (Fig. 338B): The appearance of living *Helicina talamancensis* is striking: the body is whitish-yellow throughout, the mantle pigmentation is also whitish; only the tentacles are deep black. This characteristic color is present in all live and preserved specimens studied.

Radula (Fig. 146): Cutting edge of the centrals smooth or crenulated. Comb-lateral with 8–9 cusps, cusps on marginals rather rapidly increasing in number, but with a similar effect as in *Helicina beatrix beatrix*. Radula with about 60–75 rows of teeth.

Female Reproductive System (Figs. 147, 148): Compared to *Helicina beatrix* the ascending limb of the V-organ is elongated, the receptaculum is drop-shaped. The bursa copulatrix is very irregularly lobed, the elongated provaginal sac shows a simple outline. Its stalk is short and stout. The pallial oviduct is marked by a longitudinal furrow and various transversal constrictions.



FIG. 145. Operculum of *Helicina talamancensis*, holotype, INBio 3404978; scale bar 2 mm.

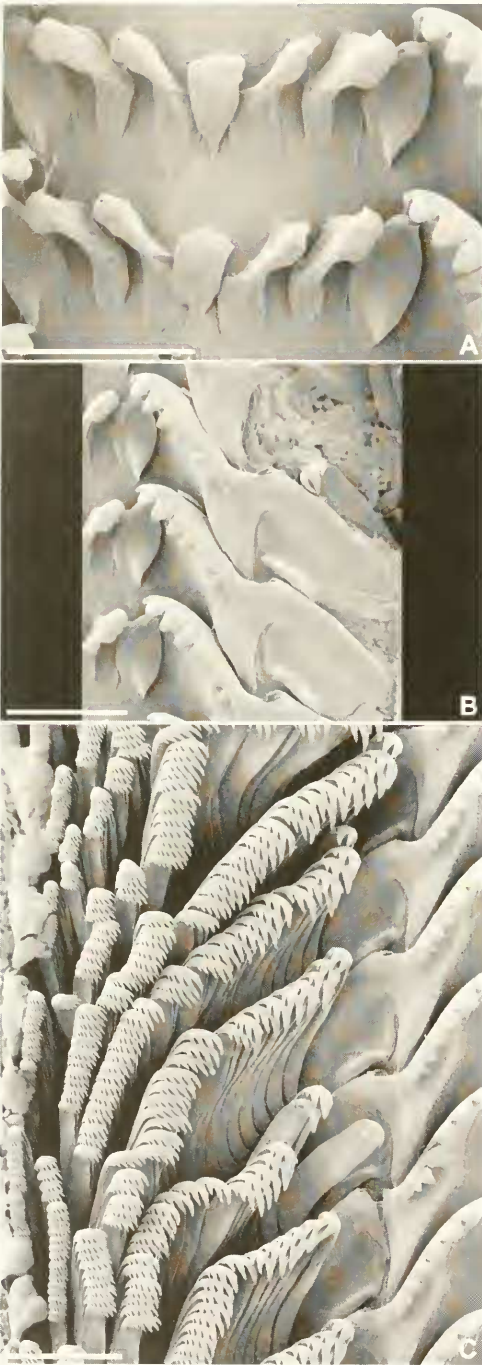


FIG. 146. Radula of *Helicina talamancensis*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 μ m.



FIG. 147. Female reproductive system of *Helicina talamancensis*, IR 1030; scale bar 1 mm.

Morphometry and Sexual Dimorphism (Table 9, Figs. 149–155)

Helicina talamancensis could not be found in high numbers, the only specimens studied anatomically are those I collected at Bajo Bonito. Populations included from the collection of INBio with sufficient individuals (Fila de Cal, Neily, Amistad, Bajo Bonito) that could not be analyzed for sex were separated as in *H. beatrix* to avoid artificial high deviations of measurements with mixed sexes.

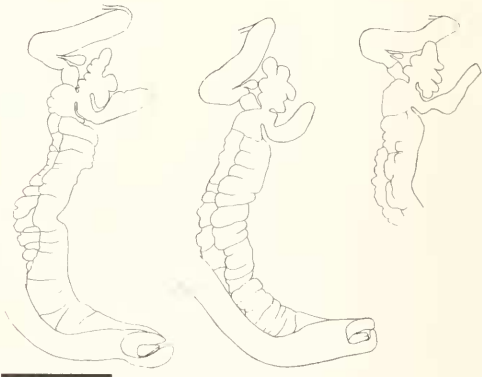


FIG. 148. Variability of the female reproductive system of *Helicina talamancensis*, IR 1030; scale bar 2.5 mm.

TABLE 9. Measurements of different populations of *Helicina talamancensis* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens; sex of individuals from Fila de Cal, Neily, Amistad and Bajo Bonito INBio not determined anatomically (see text) (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

"Bajo Bonito" (altitude 980 m) lots IR 1018, IR 1029, IR 1030, IR 1487											
	Sex	Mean value	Deviation	Min	Max	Number					
Height	f	9.03	0.33	8.48	9.61	8					
Height	m	7.81	0.18	7.50	8.22	8					
Maj. diam.	f	8.54	0.27	8.02	8.92	8					
Maj. diam.	m	7.46	0.13	7.16	7.72	8					
Min. diam.	f	7.95	0.20	7.60	8.31	8					
Min. diam.	m	6.97	0.11	6.75	7.20	8					
Outer lip	f	5.61	0.15	5.46	5.91	8					
Outer lip	m	5.12	0.17	4.80	5.41	8					
Last whorl	f	7.05	0.15	6.58	7.47	8					
Last whorl	m	6.17	0.18	5.88	6.46	8					
Col. axis	f	7.34	0.26	6.77	7.87	8					
Col. axis	m	6.29	0.19	6.03	6.68	7					
Weight	f	0.087	0.010	0.056	0.102	8					
Weight	m	0.066	0.007	0.055	0.085	8					
Volume	f	0.199	0.017	0.172	0.224	8					
Volume	m	0.130	0.008	0.115	0.145	8					

"Fila de Cal" (altitude 600–780 m) lots INBio 1480714, 1481246, 1481353, 1481564, 1482605, 1485120, 3121201, 3542530, 3542545											
	Sex	Mean value	Deviation	Min	Max	Number					
Height	f	7.73	0.17	7.35	7.98	10					
Height	m	6.80	0.21	5.82	7.17	11					
Maj. diam.	f	7.14	0.14	6.95	7.42	10					
Maj. diam.	m	6.69	0.11	6.45	6.96	11					
Min. diam.	f	6.75	0.11	6.55	6.98	10					
Min. diam.	m	6.23	0.12	6.08	6.50	11					
Outer lip	f	4.71	0.16	4.41	4.87	10					
Outer lip	m	4.46	0.08	4.26	4.62	11					
Last whorl	f	6.01	0.16	5.70	6.38	10					
Last whorl	m	5.50	0.12	5.10	5.83	11					
Col. axis	f	6.37	0.29	5.95	7.31	10					
Col. axis	m	5.65	0.20	5.29	6.27	11					

"Neily" (altitude 180 m) lot INBio 3542526											
	Sex	Mean value	Deviation	Min	Max	Number					
Height	f	7.75	0.33	7.42	8.08	2					
Height	m	6.43	0.04	6.38	6.47	2					
Maj. diam.	f	7.42	0.09	7.33	7.50	2					
Maj. diam.	m	6.60	0.06	6.54	6.65	2					
Min. diam.	f	6.90	0.17	6.73	7.06	2					
Min. diam.	m	5.95	0.10	5.85	6.04	2					
Outer lip	f	4.78	0.02	4.75	4.80	2					
Outer lip	m	4.38	0.11	4.27	4.48	2					
Last whorl	f	6.02	0.15	5.87	6.17	2					
Last whorl	m	5.15	0.20	4.95	5.35	2					
Col. axis	f	6.23	0.23	6.00	6.45	2					
Col. axis	m	5.17	0.06	5.11	5.23	2					

(Continues)

(Continued)

"Amistad" (altitude 1340–1800 m) lots INBio 1467066, 1480719, 1480725, 1481219, 1481236, 1481397, 1484619, 1485516, 1488141, 3317088, 3318194, 3542538, 3542544, 3542540							"Bajo Bonito INBio" (altitude 920 m) lots INBio 1494509, 1494642, 3389580				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	8.50	0.33	8.06	9.18	11	9.11	0.05	9.00	9.15	4
Height	m	7.26	0.17	6.88	7.67	9	8.10	0.13	7.88	8.28	5
Maj. diam.	f	8.16	0.26	7.78	8.68	11	8.47	0.10	8.33	8.62	4
Maj. diam.	m	7.20	0.21	6.38	7.50	9	7.67	0.17	7.25	7.88	5
Min. diam.	f	7.53	0.23	7.20	7.95	11	7.88	0.09	7.77	8.02	4
Min. diam.	m	6.58	0.15	5.94	6.74	9	7.08	0.12	6.77	7.22	5
Outer lip	f	5.37	0.19	5.08	5.81	11	5.62	0.10	5.42	5.79	4
Outer lip	m	4.76	0.20	4.10	5.15	8	5.14	0.14	4.88	5.40	5
Last whorl	f	6.55	0.19	6.15	6.92	11	7.12	0.07	7.02	7.20	4
Last whorl	m	5.80	0.16	5.49	6.07	9	6.25	0.10	6.09	6.48	5
Col. axis	f	6.94	0.29	6.36	7.63	11	7.29	0.13	7.12	7.55	4
Col. axis	m	5.93	0.15	5.67	6.20	9	6.51	0.08	6.41	6.64	5

"Península de Osa" (altitude 140–150 m) lots INBio 1485176, 1498766, 1498769							"Chirripó" (altitude 1300 m) lot INBio 3542536				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	8.06	0.61	7.15	8.82	3	8.16	-	-	-	1
Maj. diam.	f	8.04	0.65	7.07	8.77	3	8.21	-	-	-	1
Min. diam.	f	7.42	0.62	6.50	7.96	3	7.64	-	-	-	1
Outer lip	f	5.26	0.41	4.65	5.66	3	5.27	-	-	-	1
Last whorl	f	6.36	0.45	5.69	6.77	3	6.34	-	-	-	1
Col. axis	f	6.61	0.56	5.77	7.15	3	6.66	-	-	-	1

Morphometry: The populations show remarkable differences in size with the individuals from Fila de Cal and Neily being smallest. For each characteristic, the differences between the populations are similar, implying that the relations are about the same. Although from different altitudes and from localities relatively close to each other, the specimens from Neily and the Fila de Cal are of about the same size, which suggests rather a relation to the sites than to altitude. The few specimens from the lowlands of Península de Osa approach the shells from "Amistad" at much higher altitudes more closely in size than those from Neily or Fila de Cal.

In comparison with *Helicina beatrix beatrix*, the shell volume of the Bajo Bonito popula-

tion is smaller, but the weight is significantly higher. It confirms the impression of more solid shells in *H. talamancensis*.

Sexual Dimorphism: As in *H. beatrix* the sexes clearly diverge in all measurements, in most cases even without an overlap of the extrema (Fig. 156). The females are much bigger than the males, in volume the males are only $\frac{2}{3}$ of the females. This divergence allows the separation of individuals of unknown sex (Fig. 157), as explained under *H. beatrix beatrix*. Although containing only three specimens, the lot from Península de Osa probably consists of two females and one male, because the average is shifted to the higher value.

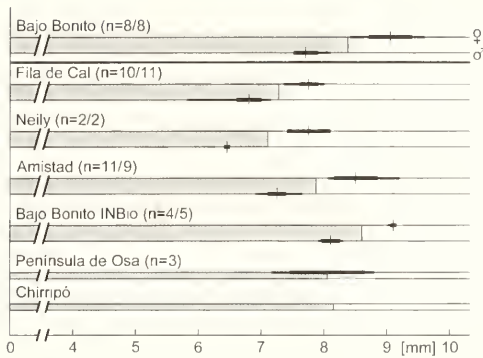


FIG. 149. Shell height of different populations of *Helicina talamancensis* in Costa Rica according to Table 9; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males or total"; upper line: females, lower line: males if separate; in between and shaded: average of both for comparison with populations of unknown sex; sex of individuals from Fila de Cal, Neily, Amistad, and Bajo Bonito INBio not determined anatomically (see text).

Contrary to most of the populations of *H. funcki* and *H. tenuis*, the smaller males also weigh less than the females.

Habitat

The species is arboreal, at the type locality specimens were found aestivating on the

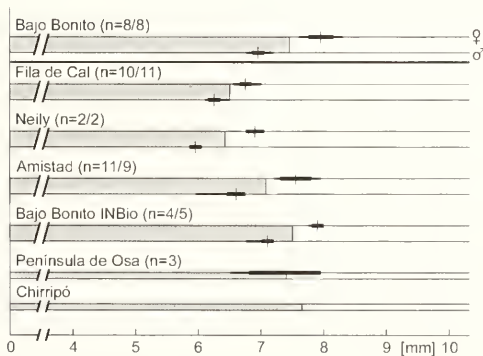


FIG. 150. Minor diameter of shell of different populations of *Helicina talamancensis* in Costa Rica according to Table 9; for explanations see Fig. 149.

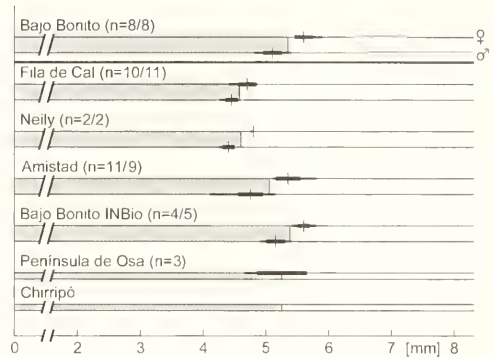


FIG. 151. Expansion of outer lip of different populations of *Helicina talamancensis* in Costa Rica according to Table 9; for explanations see Fig. 149.

lower side of leaves in the undergrowth, mainly on Heliconiaceae and different species of palms. They were more abundant during the rainy season in August than they were in February and March during the dry period. In rainy weather, individuals were also observed crawling on the upper side of leaves at night near the Wilson Botanical Garden. At several localities, *Helicina talamancensis* occurs sympatrically with *H. pitaleensis*.

Distribution (Fig. 158)

Helicina talamancensis is only known from the Pacific slopes in the southern parts of

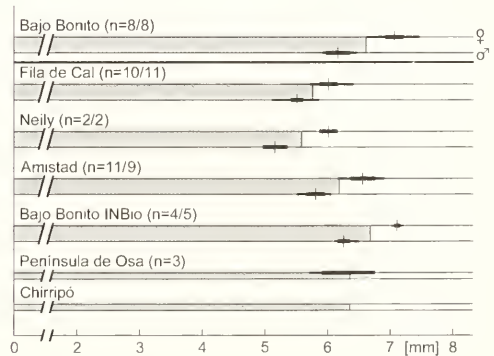


FIG. 152. Height of last whorl of different populations of *Helicina talamancensis* in Costa Rica according to Table 9; for explanations see Fig. 149.

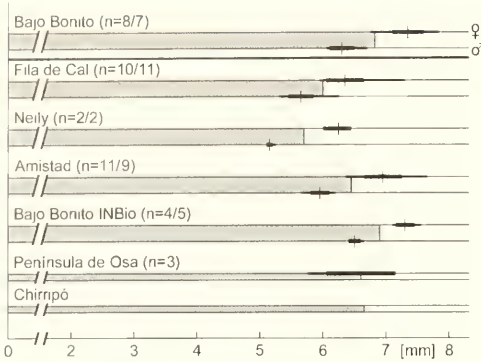


FIG. 153. Height of columellar axis of different populations of *Helicina talamancensis* in Costa Rica according to Table 9; for explanations see Fig. 149.

Costa Rica. It occurs in the lowland rain forest on the Península de Osa and near Golfito close to the coast at elevations of approximately 100–250 m. In the steep mountains of Fila Cruces and Fila de Cal and on the slopes of the southern Cordillera de Talamanca, *H. talamancensis* is found on elevations of up to 1,800 m in the cloud forest area. Although corresponding in its distribution to the southern records for *H. pitalensis*, there is no indication and no historical evidence for a more northerly occurrence of this species than the area of San Isidro. With respect to records of Helicinidae, the adjacent area of Chiriqui Province, Panama, is virtually unexplored.

Discussion

The material of *Helicina talamancensis* contains some specimens that show a completely pale orange color, whereas yellowish specimens are much more common.

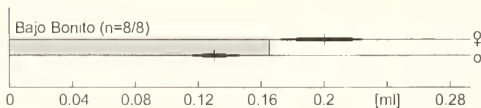


FIG. 154. Shell volume of *Helicina talamancensis* in Costa Rica according to Table 9; for explanations see Fig. 149.

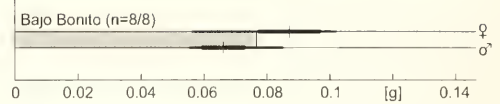


FIG. 155. Shell weight of *Helicina talamancensis* in Costa Rica according to Table 9; for explanations see Fig. 149.

The species most closely resembles *H. beatrix beatrix*, but differs in the form of the peristome. In *H. beatrix beatrix*, the outer lip is less reflexed and thinner, and the aperture is more strongly curved backwards so that the upper part appears somewhat depressed in frontal view. Furthermore, *H. talamancensis* lacks the characteristic white band directly under the suture. The color of the soft body of *H. talamancensis* is unique among Costa Rican Helicinidae.

Helicina terryae is of a nearly similar color and size. Unfortunately, this species was described from the holotype only, with the vague locality of Chiriqui Province, Panama, and there are no other similar specimens in the USNM collection (pers. comm. Dr. R. Hershler, USNM). Examination of photographs of the type (USNM 536026, not USNM 539026, as given in Rehder, 1940; pers. comm. Dr. R. Hershler) revealed that *H. terryae* displays a different outline of the last whorl in having the curvature of the periphery more towards the base. The outer lip is less reflexed, and the spire is lower. Furthermore, the surface of the shell appears to be similar to that of *H. funcki*, for example, with "irregular, oblique, and subspiral grooves", rather than to the smooth and shiny one of *H. talamancensis*.

The material of *H. beatrix* and *H. oweniana sensu* Monge-Nájera (1997) was checked in the INBio collection and was found to partially belong to *H. talamancensis*. The differences to *H. beatrix* are given above. *Helicina oweniana* differs most obviously in the distinct orange color of the outer lip and the less impressed suture.

Rehder (1940) mentioned *H. tenuis* as the most closely resembling species of *H. terryae*. From *H. talamancensis*, *H. tenuis* can easily be distinguished by its shell surface structure, rectangularly expanded outer lip, occasionally developed bands and color of shell and soft body.

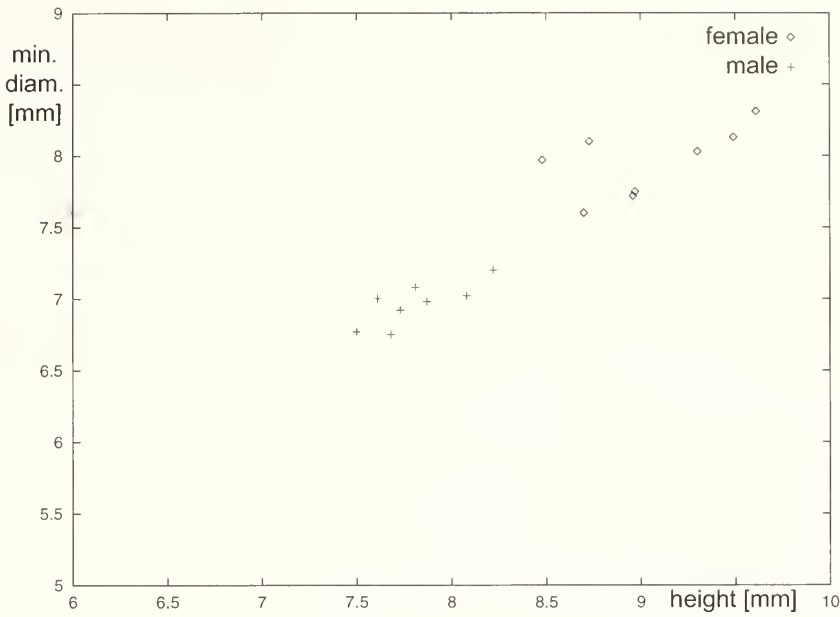


FIG. 156. Range of measurements in females and males of *Helicina talamancensis* exemplary for height and minor diameter in the population from Bajo Bonito.

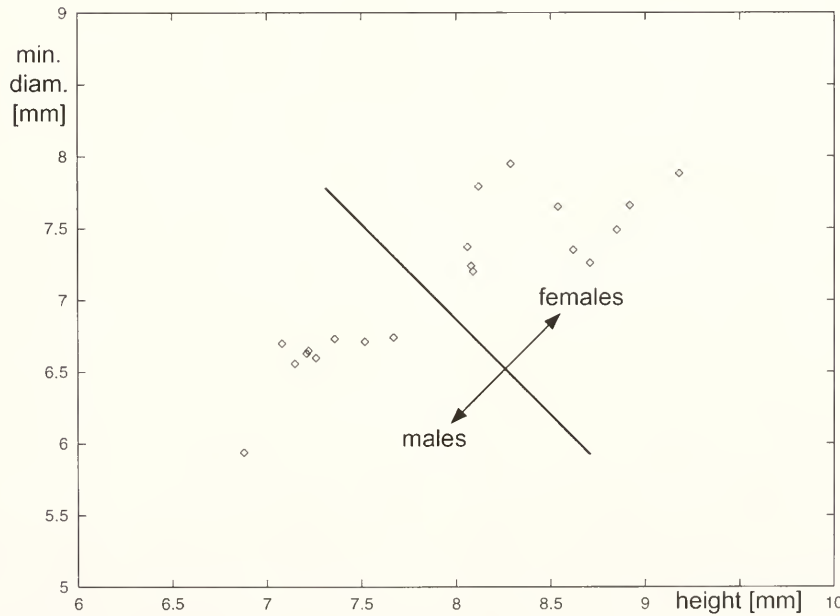


FIG. 157. Plot of measurements for height and minor diameter for individuals of *Helicina talamancensis* of unknown sex, exemplary for the population of Amistad and the separation proposed.

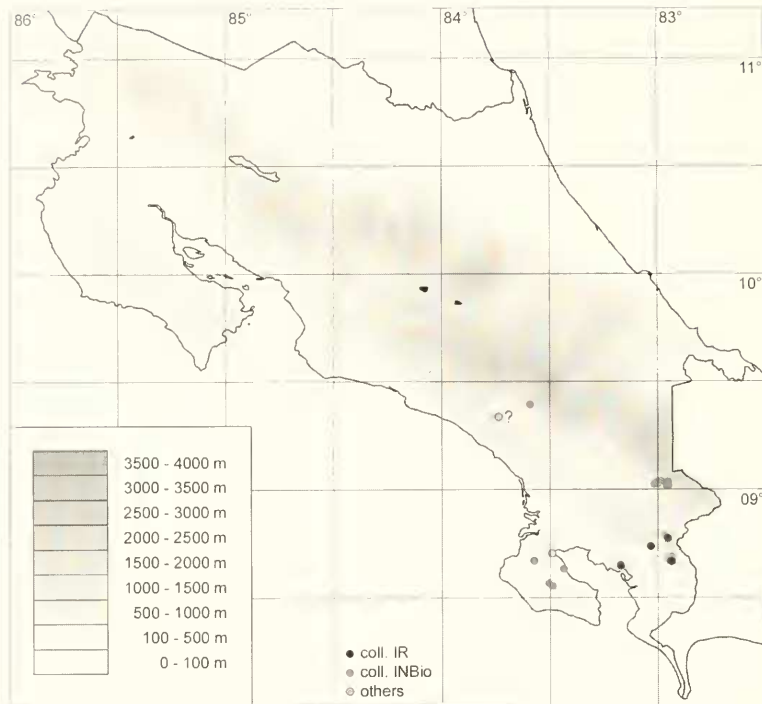


FIG. 158. Records of *Helicina talamancensis* in Costa Rica.

Helicina ("Gemma") *gemma*
Preston, 1903

Helicina oweniana var. *anozona* – Biolley, 1897: 5: Costa Rica: Tuis, 600 m [about 09°51'N, 83°35'W, Cartago Province] and las Delicias (Santa Clara), 400 m [10°57'37"N, 85°02'W, 40 m a.s.l., Alajuela Province] [non von Martens, 1876]

Helicina oweniana var. *coccinostoma* – von Martens, 1900: 605-606: E-Costa Rica: Las Delicias, near Santa Clara, 400 m [10°57'37"N, 85°02'W, 40 m a.s.l., Alajuela Province] (Biolley) [non Morelet, 1849]

Helicina oweniana var. *anozona* – von Martens, 1900: 605-606: E-Costa Rica: Las Delicias, near Santa Clara, 400 m [10°57'37"N, 85°02'W, 40 m a.s.l., Alajuela Province] (Biolley), Tuis, 600 m [about 09°51'N, 83°35'W, Cartago Province] (Pittier, Biolley) [non von Martens, 1876]

Helicina gemma Preston, 1903: 4 (with text figure)

Alcadia (*Leialcadia*) *gemma* – Wagner, 1908: 83, pl. 14, figs. 17–18

Oligyra (*Succincta*) *gemma* – Baker, 1922a: 45

Helicina oweniana – Monge-Nájera, 1997: 113: Costa Rica [in part] [non L. Pfeiffer, 1849]

Helicina beatrix – Monge-Nájera, 1997: 113: Costa Rica [in part] [non Angas, 1879]

Original Description

"Shell conical, elevated, bright yellow, apical whorls crimson, last whorl tinged with orange-scarlet for some distance from the mouth, the outer lip being also of a vivid orange-scarlet colour. Whorls 5, convex, very finely striated with lines of growth. Peristome expanded and slightly reflexed. Aperture rather high and narrow. Operculum reddish-brown, normal.

Diam. maj. 6, alt. 7 millim. Aperture (inside measurement) diam. 2.5, alt. 3 millim.

Hab. – Costa Rica.

A very beautiful and striking shell, whose nearest ally appears to be *H. oweniana*, Pfr., from Mexico; from this, however, it differs in being more globular, in the greater convexity of the whorls and in having one less, in the narrower aperture, and in the color of the outer lip (otherwise similar in both species) extending further up the body whorl than it does in *H. oweniana*."



FIG. 159. *Helicina gemma*, lectotype, BMNH 1903.5.4.2, height 7.0 mm; scale bar 2.5 mm.

Type Material

Lectotype BMNH 1903.5.4.2 "San Carlos, purchased from Mr. H.B. Preston"; 1 paralectotype ZMB 53814 "San Carlos, ex Preston", 1 paralectotype ZMB 59238 (ex Preston); 1 paralectotype ANSP 098181 "Costa Rica, San Carlos River, purchased from Preston as cotype" (Robertson et al., 1986)

According to Dance (1986), most Preston types are in the BMNH collection. Following the advice for type selection of the International Code for Zoological Nomenclature, the specimen BMNH 1903.5.4.2 is **here selected as lectotype** of *Helicina gemma* (Fig. 159). Furthermore, it was labeled by Preston as "type" and is much better preserved than the ZMB specimens suffering from Byne's disease. The specimen still possesses its operculum. I did not study the ANSP specimen.

Dimensions:

Lectotype BMNH 1903.5.4.2:

7.0/6.1/6.5/5.7/3.9/5.4/5.6 mm

Paralectotypes:

ZMB 53814: 6.0/5.4/5.8/5.0/3.5/4.5/4.7 mm

ZMB 59238: 6.7/6.0/6.2/5.5/3.7/5.0/5.4 mm

Type Locality

"Costa Rica", by type selection restricted to San Carlos [on one hand San Carlos is the old name for Ciudad Quesada, about 10°20'N, 84°26'W in Alajuela Province; on the other hand and following the data from the ANSP specimen, a river in northern Costa Rica is called Río San Carlos, bearing the name from the confluence of Río Arenal and Río Peñas Blancas near Boca de Arenal, about 10°33'N,

84°29'W, until it becomes a tributary of the Río San Juan at Boca San Carlos at the Nicaraguan border, about 10°46'30"N, 84°12'30"W in Alajuela Province, thus referring to a more northern area. However, both possible locations share the trait that they are situated on the Caribbean plain in the eastern part of Alajuela Province].

Examined Material

LEG. I. RICHLING

Guanacaste: *N of Nuevo Arenal: area of primary rain forest*, 10°33'32"N, 84°51'40"W, 800 m a.s.l.: 05.03.1999: (IR 740); "*Las Pavas*" (private reserve in preparation), secondary rain forest, about 10°33'30"N, 84°51'53"W, 800 m a.s.l., to 10°33'26"N, 84°51'57"W, 760 m a.s.l.: 05.03.1999: (IR 741); 17.08.1999: (IR 947); (IR 948); 24.02.2000: (IR 1275); (IR 1277); 27.02.2001: (IR 1460); (IR 1464); 01.03.2001: (IR 1462); 03.03.2001: (IR 1463)

Parque Nacional Guanacaste, *Volcán Cacao*, at southern slope, Estación Cacao, W-Sendero near station, forest, 10°55'35"N, 85°28'06"W, 1,110 m a.s.l., 18.03.1999: (IR 786); 09.03.2000: (IR 1333); (IR 1335)

Alajuela: *Near Volcán Arenal, trail along volcano in rainforest*: about 10°29'07"N, 84°42'55"W, 720 m a.s.l.: 24.02.1998: (IR 387); 03.03.1999: (IR 734); 01.08.1999: (IR 885); 25.02.2000: (IR 1284); about 10°33'23"N, 84°51'51"W, 800 m a.s.l.: 05.03.1997: (IR 77); (IR 76)

Limón: Siquirres, along footpath stream up *Río Siquirres* and along a southern tributary, 10°05'37"N, 83°30'32"W, 100 m a.s.l., 11.03.2001: (IR 1536); 19.03.2001: (IR 1618); (IR 1635); (IR 1650); (IR 1652)

Zona Protectora Tortuguero, *near Tortuguero*, N of village, about 10°34'N, 83°31'W, 10 m a.s.l., 16.03.2001: (IR 1621); (IR 1654)

INBIO COLLECTION

Guanacaste: *Parque Nacional Guanacaste, Estación Cacao*: 10°55'29"N, 85°28'17"W, 1,100 m a.s.l., leg. Dunia Garcia, 01.12.1995: 1 ad. (INBIO 1484977); 10°56'05"N, 85°28'14"W, 1,100 m a.s.l., leg. Dunia Garcia, 13.12.1995: 1 ad., 2 s.ads. (INBIO 1488058); 10°55'43"N, 85°28'20"W, 1,000 m a.s.l., leg. malacological staff of INBIO, 09.01.1995: 5 ads., 2 s.ads. (INBIO 1539438); Sendero Los Naranjos, 10°55'38"N, 85°28'30"W, 1,100 m a.s.l., leg. Dunia Garcia, 13.09.1995: 9 ads., 3 s.ads. (INBIO 1487886); Sendero Los Naranjos, 10°55'38"N, 85°28'30"W, 1,020 m a.s.l., leg. malacological staff of INBIO, 14.09.1995: 8 ads. (INBIO 1539463)

Parque Nacional Guanacaste, La Cruz, 9 km S de Santa Cecilia, Estación Pitilla: 10°59'25"N, 85°25'38"W, 700 m a.s.l.: leg. Petrona Rios, 22.08.1994: 1 juv. (INBIO 1480267); 1 ad. (INBIO 1480284); 10°59'33"N, 85°25'46"W, 700 m a.s.l.: leg. malacological staff of INBIO, 10.09.1993: 1 ad. (INBIO 1463737); *Lado S del Río Orosí, 10°59'25"N, 85°25'38"W, 700 m a.s.l.*: leg. Calixto Moraga, 23.08.1994: 1 ad., 2 s.ads. (INBIO 1480341); leg. Marcos Moraga, 04.04.1995: 1 ad. (INBIO 1484672); *Sendero Mena, 400 m W de la Estación Pitilla, 10°59'25"N, 85°25'51"W, 700 m a.s.l.*: leg. Calixto Moraga, 09.01.1994: 1 ad. (INBIO 1480045); *Sendero a la Fila de Orosillo, 10°59'24"N, 85°25'38"W, 700 m a.s.l.*: leg. Petrona Rios, 09.01.1994: 1 ad. (INBIO 1480270)

Parque Nacional Guanacaste, Sector Orosi (antes: Maritza); sendero Casa Fram, 10°57'40"N, 85°29'45"W, 600 m a.s.l., leg. Zaidett Barrientos, 15.07.1996: 7 ads., 1 s.ad. (INBIO 1487835)

Parque Nacional Rincón de la Vieja, Sector Santa María, 10°45'58"N, 85°18'19"W, 800 m a.s.l., leg. Dunia Garcia, 07.11.1996: 1 ad. (INBIO 1488039)

Alajuela: *Reserva Biológica San Ramón, 10°13'30"N, 84°35'17"W, 800 m a.s.l.*, leg. Gerardo Carballo, 14.12.1994: 1 ad. (INBIO 1485501)

Sector Colonia Palmareña, San Ramón, 10°13'56"N, 84°33'12"W, 760 m a.s.l., leg. Gerardo Carballo, 04.11.1995: 1 ad. (INBIO 1484803)

Limón: *Estación Cedrales: 800 m W de la Estación Cedrales, 10°31'39"N, 83°43'33"W,*

10 m a.s.l.: leg. Elias Rojas, 22.11.1996: 1 ad. (INBIO 1498586); *Finca Leiva, 1 km W de la estación Cedrales, 10°31'35"N, 83°43'33"W, 10 m a.s.l.*: leg. Elias Rojas, 17.10.1996: 1 juv. (INBIO 1501467); 3 ads. (INBIO 3398104); *Finca Montaña Grande, 10°31'39"N, 83°43'33"W, 10 m a.s.l.*: 600 m N de la estación Cedrales, leg. Elias Rojas, 18.10.1996: 3 ads., 1 s.ad. (INBIO 1501218); 500 m N de la estación Cedrales, leg. Elias Rojas, 18.11.1996: 1 ad. (INBIO 1498585) *Orillas del río Aguas Frías, 10°24'05"N, 83°36'00"W, 10 m a.s.l.*, leg. Elias Rojas, 29.11.1996: 20 ads., 15 s.ads., 8 juvs. (INBIO 1487942); 1 ad. (INBIO 1488002) *Sector Guápiles, 10°11'51"N, 83°51'22"W, 300 m a.s.l.*, leg. Alexander Alvarado Mendez, 08.03.2000: 1 ad. (INBIO 3097951)

Refugio Nacional de Vida Silvestre Barra del Colorado, Barra del Colorado, Estación Sardinas: 10°38'52"N, 83°43'52"W, 50 m a.s.l.: 10.02.1994: 1 ad., 1 s.ad. (INBIO 1484009); 12.10.1994: 1 ad. (INBIO 1484371); 16.10.1994: 1 ad. (INBIO 1484012); 22.10.1994: 6 ads. (INBIO 1485286) (all leg. Flor Araya); 10°39'11"N, 83°44'21"W, 15 m a.s.l.: 13.01.1994: 2 ads., 1 s.ad. (INBIO 1478019); 16.04.1994: 1 ad. (INBIO 1477917) (all leg. malacological staff of INBIO)

Refugio Nacional de Vida Silvestre Barra del Colorado, Pococí, Colorado, Sector Cerro Cocorí, 30 km N de Cariari, 10°35'39"N, 83°42'59"W: 160 m a.s.l.: leg. malacological staff of INBIO, 10.12.1993: 2 ads. (INBIO 1465444); 2 ads. (INBIO 1465444); 150 m a.s.l.: leg. malacological staff of INBIO, 04.10.1994: 3 ads. (INBIO 1478057); 3 ads. (INBIO 1478057); 3 ads. (INBIO 1478057)

Cartago: *Parque Nacional Barbilla*: Orilla de río Dantas, cerca de la estación principal, 09°58'23"N, 83°27'03"W, 300 m a.s.l., leg. Alexander Alvarado Mendez, 26.10.2000: 1 ad. (INBIO 3316138); Sector de la Estación de Barbilla, 09°57'58"N, 83°27'41"W, 480 m a.s.l., leg. Alexander Alvarado Mendez, 06.09.2000: 1 ad. (INBIO 3100215)

Puntarenas: *Parque Nacional Corcovado, Estación Sirena, 08°28'52"N, 83°35'32"W, 5 m a.s.l.*, leg. Mario Chinchilla, 23.03.1995: 1 ad. (INBIO 1485052)

OTHER SOURCES

COSTA RICA

Alajuela: Carriblanco [Cariblanco, about 10°17'N, 84°12'W], C.H. Lancaster (BMNH 1905.3.31.4)

Heredia: Río Frio, Standard Fruit Co., 10°20'N, 83°53'W, leg. Michael J. Corn,

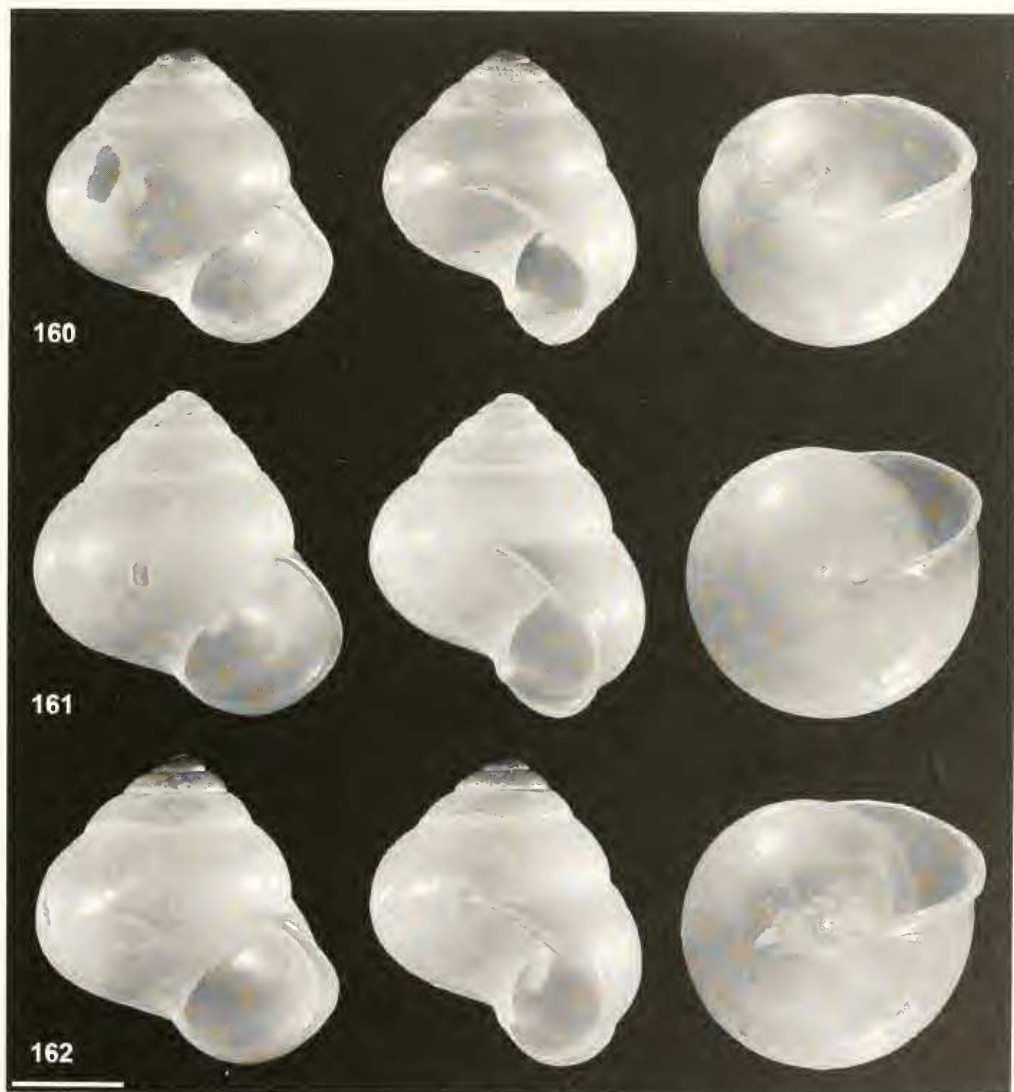
05.12.1969: 1 ad. (UF 217595); Río Frio [about 10°20'N, 83°53'W], leg. Michael J. Corn, 20.02.1970: 1 ad. (UF 217596); Costa Rica, without locality further specified: ex Sowerby & Fulton: 2 ads. (UF 243507: 2 of 3 spec.)

NICARAGUA:

Zelaya Norte: Cerro Saslaya, Bosawas, leg. Zamira Guevara M., 04.1999 (IR 3137)

Description

Shell (Figs. 160–162, 336F–H): Conical, thin and fragile, medium to small sized, semi-transparent and shiny. Color: basic color unicolored, more or less intensively yellow, apical whorls sometimes crimson; last whorl tinged with orange-brownish some distance from aperture, sometimes also at the umbilical area. Surface textured with fine and



FIGS. 160–162. *Helicina gemma*. FIG. 160. Cacao, IR 1333, height 6.6 mm. FIG. 161. Las Pavas, IR 1460, height 7.3 mm. FIG. 162. Siquirres, IR 1536, height 7.0 mm; scale bar 2.5 mm.

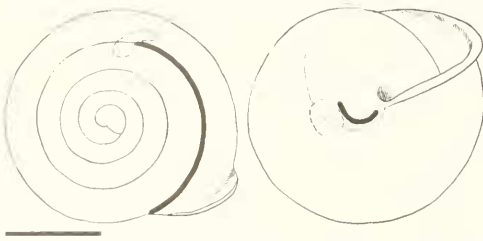


FIG. 163. Axial cleft and muscle attachments of *Helicina gemma*, IR 947; scale bar 2.5 mm.

regular growth lines (Fig. 164), causing the glossy appearance. Embryonic shell with about 1 whorl; $3\frac{5}{8}$ – $4\frac{3}{8}$ (lectotype: $4\frac{1}{4}$) subsequent whorls convex; last whorl very evenly rounded at the periphery; whorls equally extending in size, forming a very regular, pointed spire. Suture moderately impressed. Aperture oblique and curved backwards, last whorl regularly descending towards the aperture and inserting a little below the periphery. Outer lip in continuation of the whorl of a bright orange color, slightly



FIG. 164. Teleoconch surface structure of *Helicina gemma*, 2nd whorl; scale bar 100 μ m.

thickened and very narrowly expanded and reflexed. Transition to columella continuous with a slight notch. Columella slightly curved; transition to the body whorl without any groove. Basal callus very weakly developed and slightly granulated.

Internal Shell Structures: (Fig. 163)

Teleoconch Surface Structure (Fig. 164): The surface structure of *Helicina gemma* is described above representing the general scheme: about $\frac{1}{2}$ whorl exhibits transitional structure and subsequently oblique diverging grooves; the rest of the shell is smooth with only fine growth lines.

Embryonic Shell: The embryonic shell of *Helicina gemma* approaches the structure of *H. funcki* with larger pits and similarly sized interspacings. The pattern is relatively constant within a population as well as at different localities (investigated: Cacao, Las Pavas, Tortuguero, Siquirres) (Fig. 165). The diameter (range and mean value) increases with the altitude of the locality.

Diameter: 925 μ m (± 23) (900–960) ($n = 10$) (IR 786, IR 1333, Cerro Cacao); 845 μ m (± 28) (760–900) ($n = 24$) (IR 1275, Las Pavas); 808 μ m (± 25) (740–860) ($n = 32$) (IR 1635, Siquirres); 800 μ m (BMNH 1903.5.4.2, lectotype).

Operculum (Fig. 166): Very slightly calcified, calcareous plate covering only part of the outer surface. Color yellowish to horny-amber-reddish, only near the columella whitish or transparent. Columellar side slightly regular S-shaped, upper end acute and pointed, lower end continuously changing into outer margin.

Animal (Figs. 338C–E): The color of foot and head is constant in all populations, whereas the mantle pattern is subject to variation. The sole is whitish yellow; the dorsal part and upper side of the head region, including tentacles and the dorsal portion of the foot, are greyish to black. In all specimens from the Cerro Cacao and near Volcán Arenal, the mantle is unicolored and pale, whereas in the populations from Las Pavas, Tortuguero and Siquirres such forms are very rare. Instead, the mantle pigmentation displays a special pattern: a greyish-blackish basic color mottled with whitish dots. In most

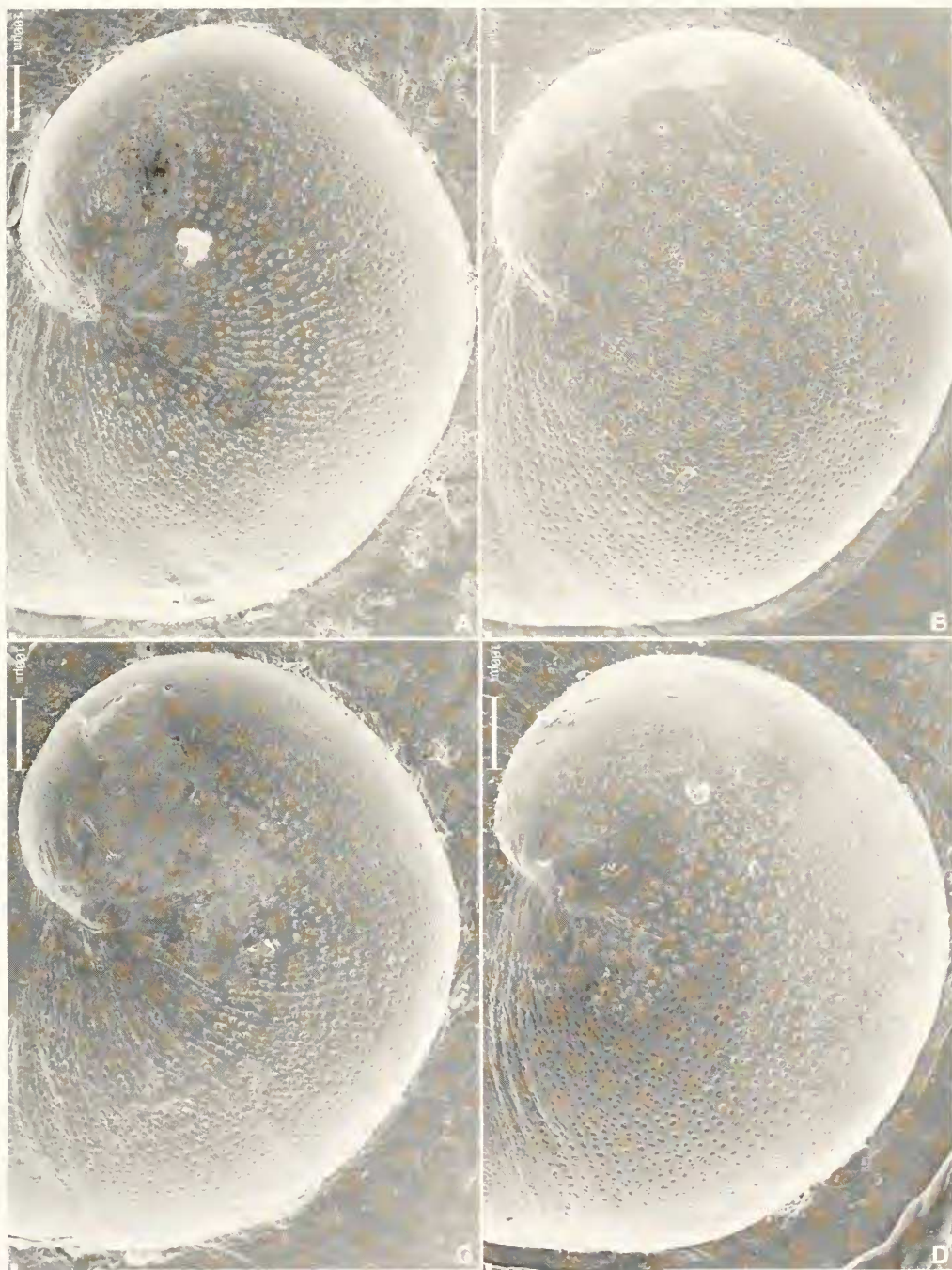


FIG. 165. Embryonic shell of *Helicina gemma*. A. Cerro Cacao, IR 786. B. Las Pavas, IR 1460. C. Tortuguero, IR 1654. D. Siquirres, IR 1618; scale bar 100 μ m.

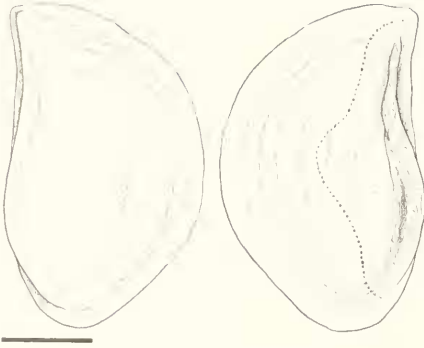


FIG. 166. Operculum of *Helicina gemma*, IR 947; scale bar 1 mm.

cases, these dots are so numerous that only a network of thin dark lines is visible. The mantle pigmentation is clearly visible through the thin shell.

Radula (Figs. 167, 168): Sometimes B- and C-central with 3–7 or about 3 cusps respectively, Figures 167A and 168 show exemplary such variations. Comb-lateral with (7–) 8–9 cusps, cusps on marginals rapidly increasing in number. Radula with about 62–85 rows of teeth.

Female Reproductive System (Figs. 169–171): The receptaculum seminis is quite large and drop-shaped. The prominently developed bursa copulatrix consists of a few relatively large, simple and equal-sized lobes, sometimes further subdivided. They are only occasionally smaller and more numerous. The provaginal sac is simple, and its stout stalk is shorter than in *Helicina funcki*. In comparison to the apical complex, the pallial oviduct is short. It is transversally constricted and often exhibits an additionally longitudinal furrow. Specimens from Las Pavas, Tortuguero and Siquirres are similar; the single female dissected from the Cerro Cacao has a smaller bursa copulatrix (Fig. 170A).

Morphometry and Sexual Dimorphism (Table 10, Figs. 172–176)

The available material of *Helicina gemma* is comparatively comprehensive, and four populations for anatomical investigations from distant sites were collected.

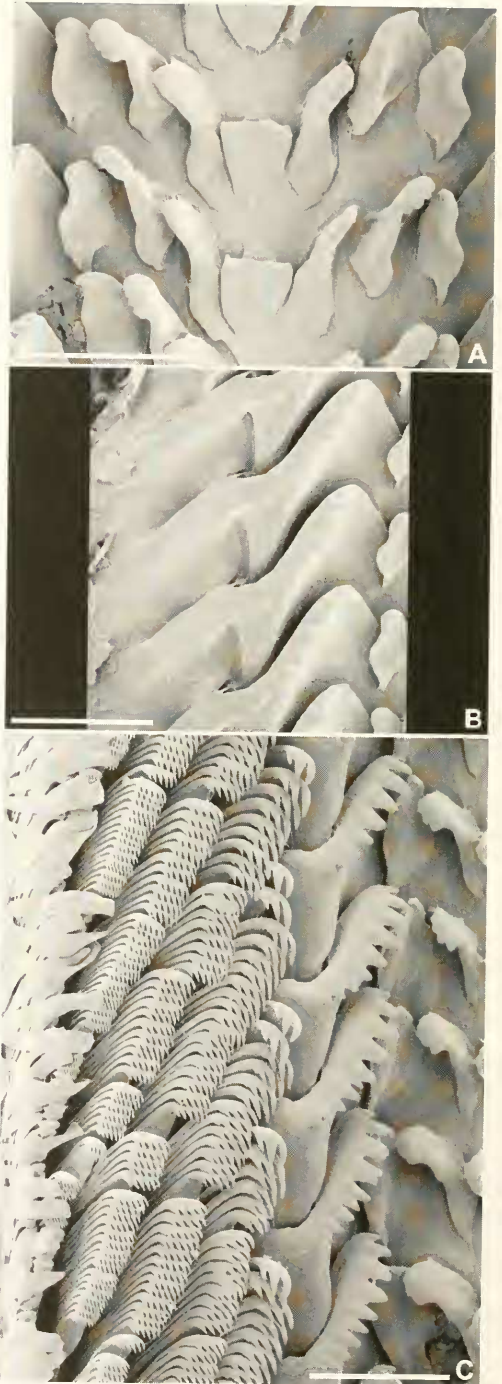


FIG. 167. Radula of *Helicina gemma*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 μ m.

Whereas the three upper localities of the collection IR and the collection INBio respectively (Figs. 172–176) belong to the northwestern Caribbean slopes, the others come from the eastern plain. The type locality is situated between these sites.

All populations included from the INBio collection (Figs. 172–176, below thick line) that could not be analyzed for their sex were separated, as in *H. beatrix*, to avoid artificially high deviations of measurements with mixed sexes.

Morphometry: The variations among the different populations for the different measurements are quite constant. The size differences correspond to the origin of the specimens. "Cacao" (IR and INBio), "Las Pavas", "Volcán Arenal" and "Orosi" are very similar to each other; only the shell size of the population "Pitilla" is somewhat smaller. Except for Tortuguero which is very close to the sea, *Helicina gemma* becomes bigger in the northeastern Caribbean lowlands. More to the south, near southern limit of known distribution, the size declines (Siquirres). The lectotype, higher than the average shell of the populations compared, has an intermediate size, suggesting that it is a female. As in some samples of *H. funcki*, the corresponding mean values of the two samples from "Cacao" treated separately support the reliability of results gained with small samples sizes.

Following the suggestion that the shells become larger in the lowlands, the average minor diameter was plotted against the altitude of the sites (Fig. 178). The values indicate a slight decline of the size with

increasing altitude. The difference amounts about 10% of the shell size of the population with the largest individuals, which is only 5% less than in *H. funcki* but which is yet found up to 1,500 m.

Sexual Dimorphism: All measurements clearly show a different range for both sexes, with the females being bigger. Only in populations with a high sample size (Siquirres, Las Pavas) do the extrema overlap a little, this being illustrated for the original set of data of height and minor diameter for the populations "Las Pavas" and "Siquirres" (Figs. 179, 180). The volume of the males is only about $\frac{2}{3}$ of that of the females. The differences displayed for the populations are very constant for each measurement. As explained in *H. beatrix*, the well-developed sexual dimorphism allows a separation of sets of mixed data. (illustrated for Río Aguas Frias, Fig. 181)

The lectotype is assumed to be female, because it seems very unlikely that the type (type lot) is extraordinarily big in a species of low variation. Furthermore, the paralectotypes are smaller.

Habitat

Helicina gemma is an arboreal species, mainly climbing and aestivating on the lower



FIG. 168. Radula of *Helicina gemma*, centrals; scale bar 50 μ m.



FIG. 169. Female reproductive system of *Helicina gemma*, IR 1275; scale bar 1 mm.

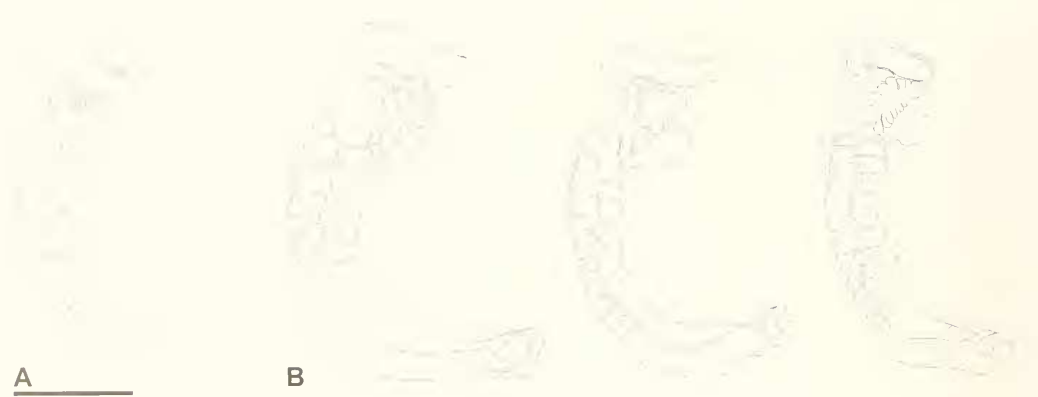


FIG. 170. Variability of the female reproductive system of *Helicina gemma*, populations from A. Cerro Cacao, IR 786. B. Las Pavas, IR 947, IR 1275; scale bar 2 mm.

and sometimes upper side of leaves. As observed for *H. beatrix*, a special preference of certain plant species could not be observed. The predominant presence appears to depend on the species composition of the undergrowth on whose leaves the species were found. On the Cerro Cacao several small-leaved plants provide a crawling and foraging surface for the snails, whereas in Las Pavas Heliconiaceae and different palms represent a good place to search for *H. gemma*. In Siquirres, specimens were often seen aestivating also on the upper surface of nearly every kind of plant composing the secondary growth near a small creek. On one occasion, the species was found in dead decomposing *Cecropia*-leaves on the ground in the rain forest.

Distribution

The species is limited to southern Central America. The most northern record comes from the Cerro Saslaya in Nicaragua, adjacent to the Costa de Miskitos stretching along the Caribbean coast. The southern limit is reached around Siquirres and Parque Nacional de Barbilla, the northeastern foothills of the Cordillera de Talamanca. *Helicina gemma* possibly occurs a little further the south, but the data suggest that it is finally absent in the Valle de Talamanca or even in the Valle de Estrella, because the lower regions which are normally inhabited by the species have been fairly well investigated, and *H. gemma* has not been reported.



FIG. 171. Variability of the female reproductive system of *Helicina gemma*, populations from A. Tortuguero, IR 1654. B. Siquirres, IR 1652; scale bar 2 mm.

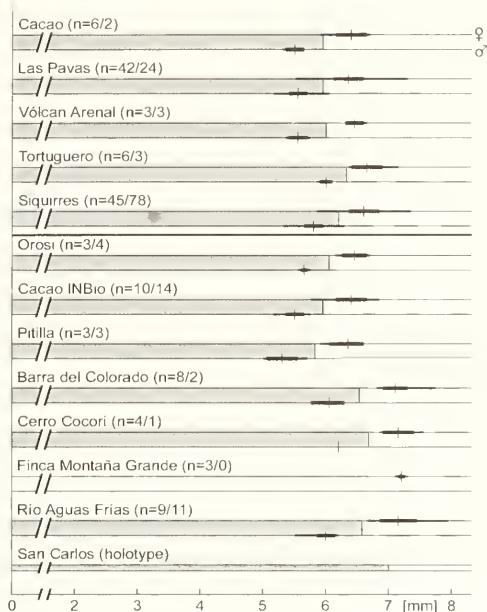


FIG. 172. Shell height of different populations of *Helicina gemma* in Costa Rica according to Table 10; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males"; upper line: females, lower line: males; in between and shaded: average of both for comparison with populations of unknown sex; sex of individuals from Orosi, Cacao INBio, Pitilla, Barra del Colorado, Cerro Cocorí, Finca Montaña Grande, and Rio Aguas Frias not determined anatomically (see text).

In Costa Rica, *H. gemma* is confined to the Caribbean plain and the adjacent mountain slopes (Fig. 182). The highest altitude is reached in the northern Cordillera de Guanacaste on the Cerro Cacao at about 1,100 m, where it just crosses the chain of volcanoes. In this region, the higher elevated areas still provide a suitable climate on the otherwise drier Pacific slopes. The absence in the intensively searched area around Monteverde and its presence in the region of the Volcán Arenal and San Ramón at lower altitudes provides evidence that *H. gemma* does not occur much above 1,200 m. In the Caribbean lowlands it is or was probably fairly well distributed although not directly visible on the map. On one hand, vast areas have been deforested and used for agriculture, most probably causing a massive habitat loss, because the species has thus far only been found in pri-

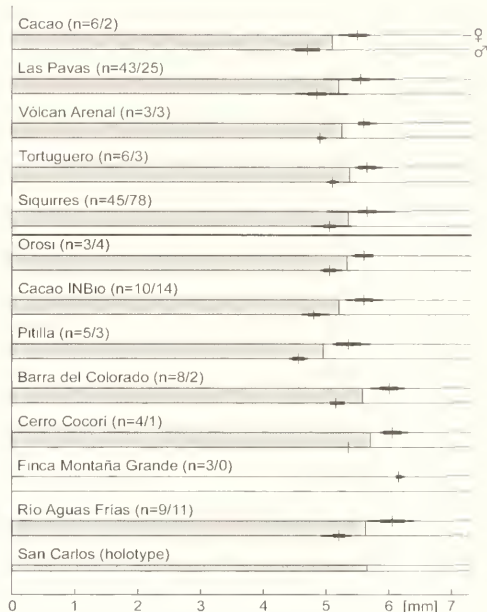


FIG. 173. Minor diameter of shell of different populations of *Helicina gemma* in Costa Rica according to Table 10; for explanations see Fig. 172.

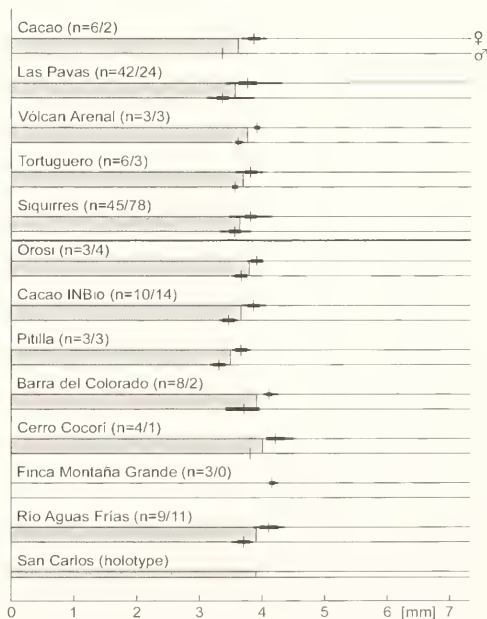


FIG. 174. Expansion of outer lip of different populations of *Helicina gemma* in Costa Rica according to Table 10; for explanations see Fig. 172.

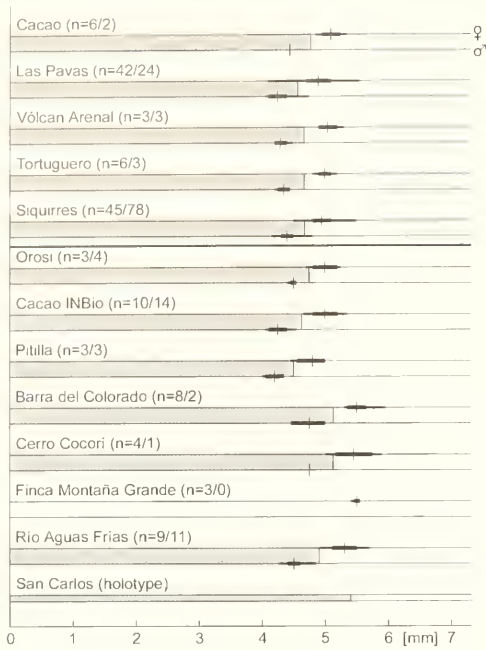


FIG. 175. Height of last whorl of different populations of *Helicina gemma* in Costa Rica according to Table 10; for explanations see Fig. 172.

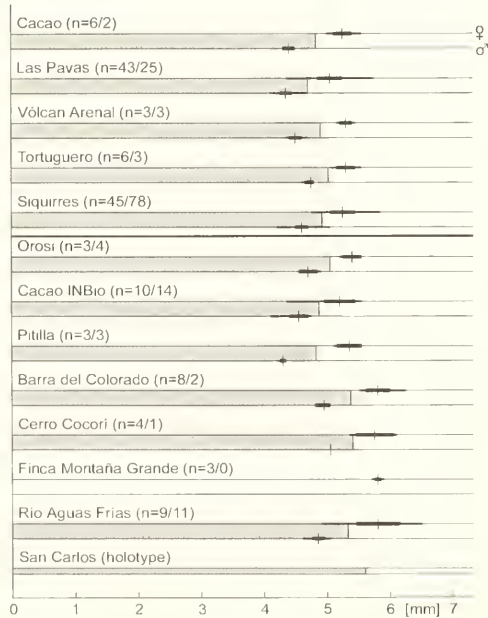


FIG. 176. Height of columellar axis of different populations of *Helicina gemma* in Costa Rica according to Table 10; for explanations see Fig. 172.

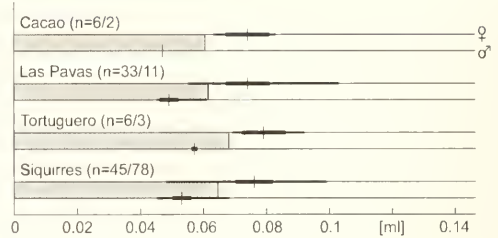


FIG. 177. Shell volume of different populations of *Helicina gemma* in Costa Rica according to Table 10; for explanations see Fig. 172.

mary or secondary forest or forest-like habitats. On the other hand, investigations (especially INBio's) focus on protected areas compassing mainly mountainous terrain (watersheds and volcanoes). The only exception for the lowlands is the zone of Colorado – Tortuguero on the NE coast. The pattern of distribution is very similar to that of *H. funcki*, except for the fact that the latter has a wider range and obviously a higher ecological tolerance.

Discussion

The color of the shells varies among the different populations in respect to the basic whorl color. Specimens from the Arenal area (volcano and Las Pavas) are pale yellow to even whitish-transparent, whereas the populations of the Caribbean lowlands (Siquirres, Tortuguero, Cerro Cocorí, Barra del Colorado) and Pitilla are bright yellow. Only specimens from the Cacao exhibit a strong tendency towards brownish shells, which is otherwise only very exceptionally observed in the Siquirres population (about 3 out of 120 specimens). The orange aperture is a common and constant character of all specimens, as is the crimson apex of a part of each population.

Preston (1903) compared *Helicina gemma* to *H. oweniana* and recognized the greater convexity (deeper impressed sutures) and fewer whorls. He also stated that the orange color of the outer lip extends further up the last whorl. This is verified by the study of syntypes of *H. oweniana*. Furthermore, *Helicina oweniana* is more solid and larger, the outer lip is very straight and perpendicularly expanded, whereas in *H. gemma* it is narrowly reflexed and curved backwards.

At the time of von Martens' (1890–1901) and Biolley's (1897) reports on the Costa Rican land molluscs, *Helicina oweniana* and subspe-

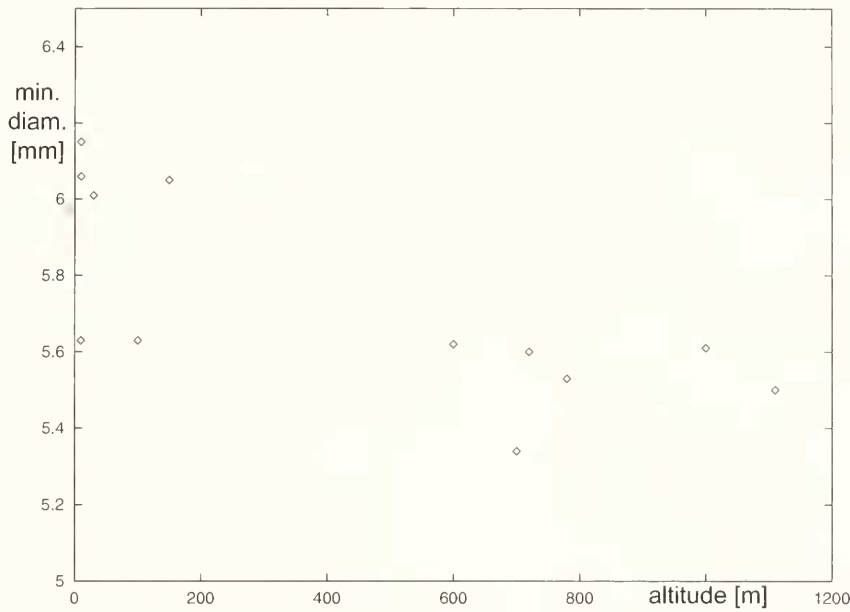


FIG. 178. Relation of minor shell diameter (females used) to altitude of the locality of the different populations of *Helicina gemma* in Costa Rica.

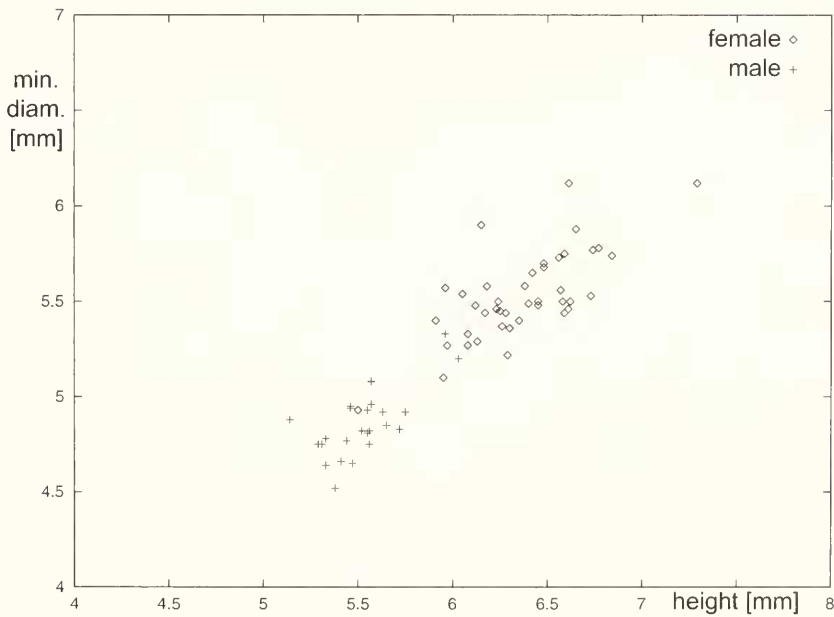


FIG. 179. Range of measurements in females and males of *Helicina gemma* exemplary for height and minor diameter in the population from Las Pavas.

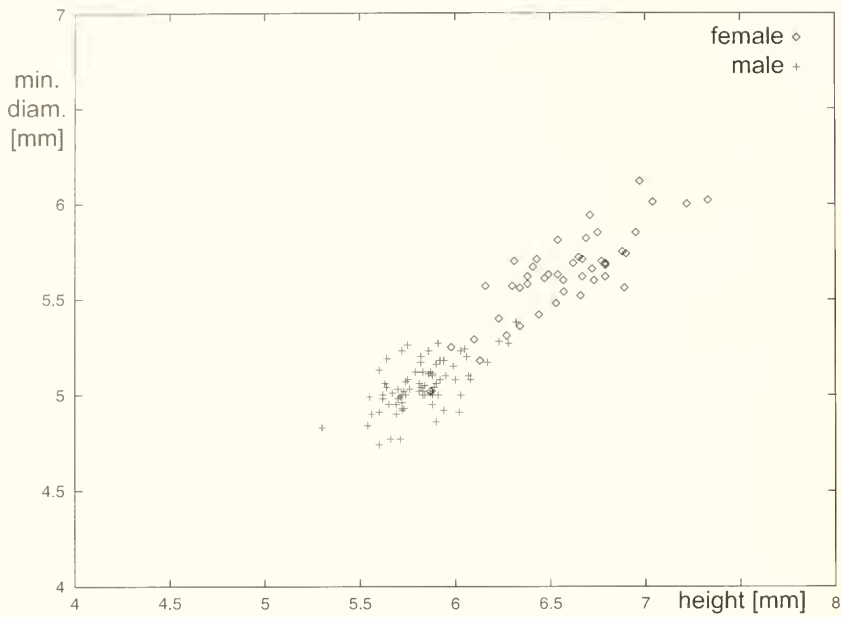


FIG. 180. Range of measurements in females and males of *Helicina gemma* exemplary for height and minor diameter in the population from Squirres.

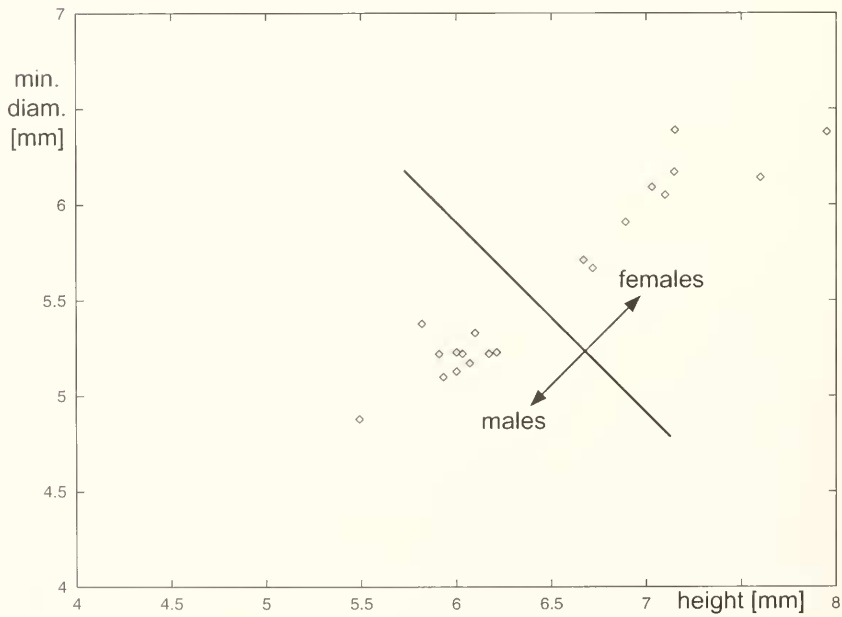


FIG. 181. Plot of measurements for height and minor diameter for individuals of *Helicina gemma* of unknown sex, exemplary for the population of Río Aguas Frías and the separation proposed.

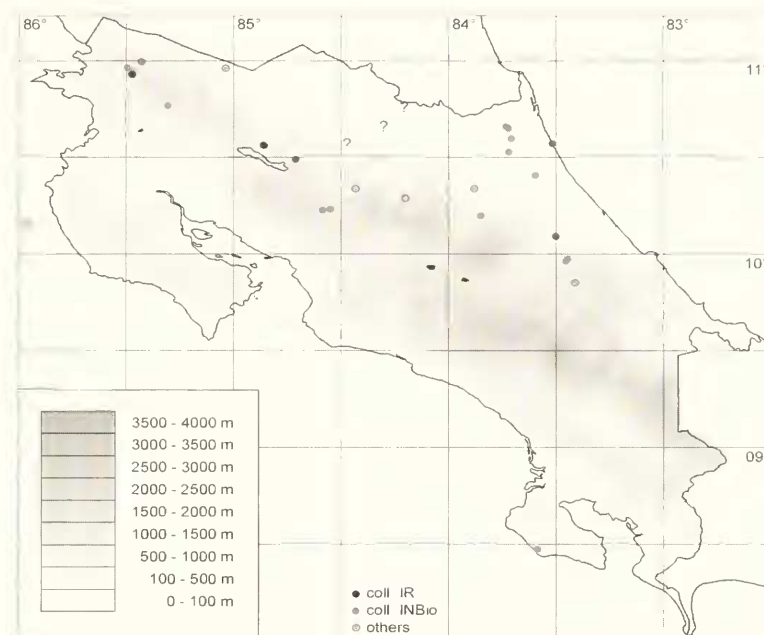
FIG. 182. Records of *Helicina gemma* in Costa Rica.

TABLE 10. Measurements of different populations of *Helicina gemma* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens; sex of individuals of all populations included from the collection of INBio (both lower rows and Orosi) not determined anatomically (see text) (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

"Tortuguero" (altitude 10 m) lots IR 1621, IR 1654							"Siquirres" (altitude 100 m) lots IR 1536, IR 1618, IR 1635, IR 1650, IR 1652				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	6.67	0.25	6.33	7.13	6	6.58	0.24	5.87	7.33	45
Height	m	6.00	0.09	5.87	6.08	3	5.82	0.14	5.30	6.32	78
Maj. diam.	f	6.05	0.15	5.90	6.28	6	6.06	0.18	5.38	6.55	45
Maj. diam.	m	5.50	0.05	5.43	5.56	3	5.49	0.12	5.20	5.83	78
Min. diam.	f	5.63	0.13	5.45	5.88	6	5.63	0.16	5.02	6.12	45
Min. diam.	m	5.12	0.06	5.02	5.18	3	5.05	0.10	4.74	5.38	78
Outer lip	f	3.80	0.12	3.57	3.98	6	3.81	0.12	3.43	4.13	45
Outer lip	m	3.55	0.05	3.50	3.62	3	3.54	0.08	3.32	3.79	78
Last whorl	f	4.98	0.12	4.82	5.22	6	4.96	0.16	4.48	5.52	45
Last whorl	m	4.34	0.09	4.22	4.47	3	4.42	0.10	4.13	4.81	78
Col. axis	f	5.31	0.17	5.03	5.57	6	5.25	0.19	4.74	5.84	45
Col. axis	m	4.74	0.09	4.60	4.82	3	4.59	0.12	4.19	5.04	78
Weight	f	0.015	0.002	0.012	0.018	6	0.022	0.003	0.012	0.032	45
Weight	m	0.015	0.001	0.014	0.017	3	0.019	0.004	0.011	0.031	78
Volume	f	0.079	0.007	0.069	0.092	6	0.076	0.006	0.048	0.099	45
Volume	m	0.057	0.001	0.056	0.058	3	0.053	0.003	0.045	0.068	78

(Continues)

(Continued)

"Cacao" (altitude 1110 m) lots IR 786, IR 1333							"Las Pavas" (altitude 760-800 m) lots IR 947, IR 948, IR 1275, IR 1460, IR 1462, IR 1463				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	6.41	0.24	5.90	6.72	6	6.36	0.25	5.50	7.29	42
Height	m	5.48	0.17	5.31	5.64	2	5.53	0.15	5.14	6.03	24
Maj. diam.	f	5.92	0.17	5.66	6.16	6	5.98	0.19	5.42	6.71	43
Maj. diam.	m	5.27	0.10	5.17	5.37	2	5.31	0.16	5.03	5.90	25
Min. diam.	f	5.50	0.16	5.21	5.70	6	5.53	0.17	4.93	6.12	43
Min. diam.	m	4.68	0.22	4.46	4.90	2	4.85	0.13	4.52	5.33	25
Outer lip	f	3.85	0.12	3.65	4.03	6	3.77	0.13	3.38	4.28	42
Outer lip	m	3.37	0.00	3.37	3.37	2	3.37	0.12	3.11	3.86	24
Last whorl	f	5.10	0.14	4.84	5.33	6	4.90	0.20	4.10	5.55	42
Last whorl	m	4.47	0.01	4.46	4.48	2	4.26	0.17	4.03	4.75	24
Col. axis	f	5.25	0.14	5.02	5.57	5	5.05	0.20	4.34	5.77	43
Col. axis	m	4.39	0.10	4.29	4.48	2	4.34	0.12	4.08	4.72	25
Weight	f	0.017	0.004	0.011	0.024	6	0.016	0.002	0.011	0.021	42
Weight	m	0.015	0.003	0.012	0.017	2	0.014	0.003	0.007	0.025	21
Volume	f	0.074	0.007	0.063	0.083	6	0.073	0.007	0.050	0.103	42
Volume	m	0.047	0.000	0.047	0.047	1	0.047	0.003	0.040	0.061	21

"Vólcan Arenal" (altitude 720 m) lots IR 387, IR 740, IR 885, IR 1284							"Orosi" (altitude 600 m) lot INBio 1487835				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	6.46	0.16	6.32	6.70	3	6.47	0.20	6.17	6.69	3
Height	m	5.54	0.15	5.35	5.77	3	5.63	0.06	5.56	5.74	4
Maj. diam.	f	6.08	0.10	5.92	6.16	3	6.17	0.24	5.81	6.53	3
Maj. diam.	m	5.39	0.04	5.32	5.43	3	5.49	0.15	5.20	5.75	4
Min. diam.	f	5.60	0.12	5.50	5.78	3	5.62	0.16	5.38	5.77	3
Min. diam.	m	4.92	0.06	4.84	5.01	3	5.04	0.10	4.89	5.24	4
Outer lip	f	3.90	0.05	3.85	3.97	3	3.89	0.09	3.75	3.98	3
Outer lip	m	3.61	0.06	3.54	3.70	3	3.63	0.11	3.48	3.76	4
Last whorl	f	5.07	0.16	4.90	5.31	3	4.98	0.20	4.69	5.25	3
Last whorl	m	4.32	0.10	4.22	4.48	3	4.48	0.07	4.40	4.56	4
Col. axis	f	5.28	0.10	5.13	5.43	3	5.40	0.14	5.19	5.54	3
Col. axis	m	4.50	0.12	4.36	4.68	3	4.68	0.15	4.56	4.90	3
Weight	f	0.022	0.000	0.022	0.022	1	-	-	-	-	-
Weight	m	-	-	-	-	-	-	-	-	-	-

(Continues)

cies were the only known Central American orange-lipped Helicinidae, which is why they most likely assigned their Costa Rican orange-lipped Helicinidae to the subspecies *H. oweniana coccinostoma* or *H. o. anozona*. Both probably synonymous subspecies are more globular, with whorls a little more convex

than the nominal subspecies, thus rather resembling *H. gemma*. But the differences to *H. gemma* mentioned above refer to the subspecies as well. Unfortunately, the original material of these records has not yet been rediscovered to check this assumption, but it seems plausible.

(Continued)

"Cacao INBio" (altitude 1000–1100 m) lots INBio 1484977, 1487886, 1488058, 1539438, 1539463						"Pitilla" (altitude 700 m) lots INBio 1463737, 1480045, 1480270, 1480284, 1480341, 1484672					
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	6.38	0.23	5.74	6.84	10	6.33	0.28	5.91	6.59	3
Height	m	5.52	0.15	5.16	5.77	14	5.32	0.24	5.02	5.68	3
Maj. diam.	f	5.99	0.15	5.52	6.22	10	5.75	0.23	5.44	6.10	5
Maj. diam.	m	5.24	0.08	5.03	5.46	14	4.85	0.10	4.71	4.96	3
Min. diam.	f	5.61	0.16	5.29	5.92	10	5.34	0.20	5.08	5.69	5
Min. diam.	m	4.80	0.11	4.60	5.04	14	4.56	0.09	4.42	4.66	3
Outer lip	f	3.85	0.10	3.65	4.04	10	3.64	0.11	3.50	3.81	3
Outer lip	m	3.43	0.08	3.28	3.61	14	3.30	0.10	3.17	3.44	3
Last whorl	f	5.00	0.18	4.67	5.35	10	4.80	0.24	4.44	4.98	3
Last whorl	m	4.27	0.14	4.05	4.53	14	4.22	0.16	3.98	4.37	3
Col. axis	f	5.19	0.23	4.35	5.55	10	5.36	0.18	5.09	5.57	3
Col. axis	m	4.54	0.14	4.10	4.77	14	4.30	0.06	4.21	4.35	3

"Barra del Colorado" (altitude 15–50 m) lots INBio 1477917, 1484009, 1484012, 1484371, 1485286						"Cerro Cocorí" (altitude 150 m) lots INBio 1465444, 1478057					
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	7.10	0.22	6.81	7.75	8	7.16	0.26	6.83	7.55	4
Height	m	6.03	0.29	5.74	6.32	2	6.21	0.00	6.21	6.21	1
Maj. diam.	f	6.44	0.15	6.07	6.60	8	6.57	0.20	6.32	6.88	4
Maj. diam.	m	5.55	0.17	5.38	5.72	2	5.88	0.00	5.88	5.88	1
Min. diam.	f	6.01	0.14	5.69	6.27	8	6.05	0.16	5.83	6.32	4
Min. diam.	m	5.16	0.13	5.03	5.29	2	5.33	0.00	5.33	5.33	1
Outer lip	f	4.12	0.07	4.02	4.26	8	4.18	0.17	4.03	4.52	4
Outer lip	m	3.68	0.28	3.40	3.95	2	3.82	0.00	3.82	3.82	1
Last whorl	f	5.50	0.17	5.31	5.95	8	5.45	0.28	5.02	5.91	4
Last whorl	m	4.73	0.29	4.44	5.02	2	4.73	0.00	4.73	4.73	1
Col. axis	f	5.80	0.18	5.49	6.23	8	5.77	0.28	5.36	6.12	4
Col. axis	m	4.93	0.13	4.80	5.05	2	5.03	0.00	5.03	5.03	1

"Finca Montaña Grande" (altitude 10 m) lot INBio 1501218						"Río Aguas Frías" (altitude 10 m) lot INBio 1487942					
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	7.20	0.07	7.10	7.30	3	7.14	0.29	6.67	7.95	9
Height	m	-	-	-	-	-	5.98	0.14	5.49	6.21	11
Maj. diam.	f	6.63	0.07	6.53	6.74	3	6.56	0.10	6.22	6.78	9
Maj. diam.	m	-	-	-	-	-	5.64	0.10	5.30	5.91	11
Min. diam.	f	6.15	0.06	6.12	6.24	3	6.06	0.20	5.67	6.39	9
Min. diam.	m	-	-	-	-	-	5.19	0.09	4.88	5.38	11
Outer lip	f	4.17	0.06	4.08	4.26	3	4.11	0.13	3.86	4.35	9
Outer lip	m	-	-	-	-	-	3.69	0.09	3.48	3.85	11
Last whorl	f	5.48	0.04	5.42	5.53	3	5.32	0.21	4.90	5.72	9
Last whorl	m	-	-	-	-	-	4.50	0.12	4.26	4.84	11
Col. axis	f	5.82	0.06	5.72	5.88	3	5.81	0.35	4.88	6.49	9
Col. axis	m	-	-	-	-	-	4.85	0.11	4.58	5.03	11

The records for *H. oweniana* and *H. beatrix* by Monge-Nájera (1997) were checked in the INBio-collection and partially belong to *H. gemma*. For differences to *H. beatrix riopejensis* n. subsp. and *H. montevertensis* n. sp. see under these taxa.

***Helicina* ("Gemma") *montevertensis*
Richling, n. sp.**

Helicina oweniana – Monge-Nájera, 1997: 113: Costa Rica [in part] [non L. Pfeiffer, 1849]

Helicina beatrix – Monge-Nájera, 1997: 113: Costa Rica [in part] [non Angas, 1879]

Type Material

Holotype: INBio 3542627, female (leg. I. Richling, 24.02.1999, ex IR 634)

Paratype 1: INBio 3542628, male (same data as holotype, 27.07.1999, ex IR 844)

Paratype 2: ZMB 103884, female (same data as holotype)

Paratype 3: ZMB 103885, male (same data as paratype 1)

Dimensions:

Holotype: 6.6/6.2/6.5/5.8/3.6/4.8/5.2 mm

Paratype 1: 5.9/5.5/5.8/5.1/3.6/4.6/4.8 mm

Paratype 2: 6.8/6.5/6.8/5.9/4.0/5.0/5.4 mm

Paratype 3: 5.6/5.7/6.1/5.1/3.6/4.6/4.5 mm

Type Locality

NW-Costa Rica, Puntarenas Province, Cordillera de Tilarán, near Monteverde, Zona Protectora Arenal-Monteverde, Reserva Biológica Bosque Nuboso Monteverde, Sendero Bosque Nuboso, about 10°18'08"N, 84°47'41"W, 1,550 m a.s.l., cloud forest.

Type Material of Synonymous Taxa or Similar Species

Helicina merdigera L. Pfeiffer, 1855

Helicina merdigera L. Pfeiffer, 1855: 102: Mexico: Vera Cruz (leg. Sallé, coll. Hugh Cuming)

Type Material: BMNH 20010752: leg. Sallé, coll. Hugh Cuming

The lot contains three specimens, of which one is completely fragmented except for the aperture with the operculum still inside. The

two remaining shells are very similar to each other. The species was neither figured by the author nor does the description give any useful hints for the identification of the type. The slightly larger shell is **here selected as lectotype** (Fig. 183), the denticle at the transition of the basal outer lip into the columella is stronger developed. Whereas the paralectotype (Fig. 184) is whitish, it shows a tinge of yellowish-brown.

Dimensions:

Lectotype 20010752.1:

5.0/5.1/5.4/4.7/2.9/3.7/4.0 mm

Paralectotype 20010752.2–3 (latter fragmented): 4.5/5.0/5.3/4.5/3.0/3.4/3.7 mm

Type Locality: "Vera Cruz, Mexico".

Helicina fragilis Morelet, 1851

Helicina fragilis Morelet, 1851: 17 (not figured)

Type Material: BMNH 1893.2.4.809–12, coll. Morelet, purchased from H. Fulton

The Morelet collection was bought by H. Fulton and subsequently purchased by the BMNH. The "type" among the four syntypes (Figs. 185, 186) is marked with an "x" on the shell. This specimen is **here selected as lectotype** (Fig. 185). It matches best the dimensions given by Morelet. It is neither the largest nor the smallest specimen of the type lot.

Dimensions:

Lectotype 1893.2.4.809:

6.0/5.5/5.7/5.1/3.4/4.2/4.9 mm; 5 teleoconch whorls

Paralectotypes 1893.2.4.810–12:

7.2/6.6/7.0/6.1/4.1/5.2/5.9 mm; 4⁷/₈ teleoconch whorls

5.9/5.6/6.0/5.2/3.5/4.3/4.7 mm; 4³/₈ teleoconch whorls

5.2/5.2/5.6/4.8/3.2/3.9/4.1 mm; 4¹/₄ teleoconch whorls

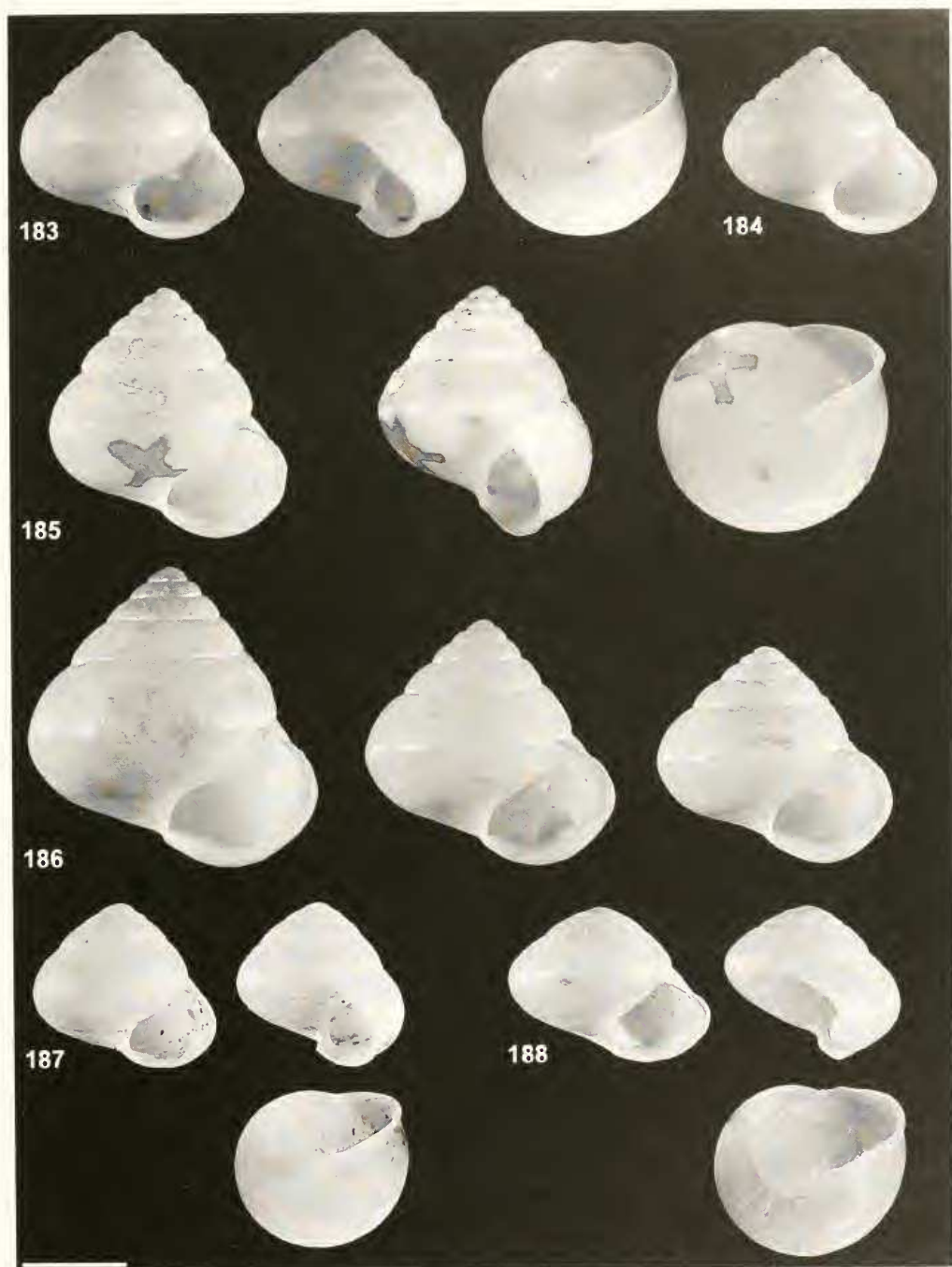
Type Locality: "sylvas Petenenses" [Guatemala: Petén Department].

Helicina mohriana L. Pfeiffer, 1861

Helicina mohriana L. Pfeiffer, 1861: 172–173

Type Material: Not located, probably lost.

Type Locality: Mexico, Orizaba (leg. Mohr) [State of Vera Cruz]



FIGS. 183–188. *Helicina* spp. FIG. 183. *Helicina merdigera*, BMNH 20010752.1, lectotype, height 5.0 mm. FIG. 184. *Helicina merdigera*, BMNH 20010752.2, paralectotype, height 4.5 mm. FIG. 185. *Helicina fragilis*, BMNH 1893.2.4.809, lectotype, height 6.0 mm. FIG. 186. *Helicina fragilis*, BMNH 1893.2.4.810–812, paralectotypes, height 7.2, 5.9, 5.2 mm. FIG. 187. *Helicina elata*, syntype, NHMB 15269, height 4.0 mm. FIG. 188. *Helicina diaphana*, probable syntype, BMNH 196282, height 3.7 mm; scale bar 2.5 mm.

Helicina elata Shuttleworth, 1852

Helicina elata Shuttleworth, 1852: 304

Type Material: Syntype NHMB 15269: leg. Jacot-Guillarmod (Fig. 187)

Shuttleworth stated "specimina pauca vidi", but his collection in the NHMB contains only a single specimen. He probably exchanged the others.

Dimensions:

Syntype: 4.0/4.3/4.3/3.8/2.4/2.9/3.1 mm

Type Locality: Mexico: Vera Cruz: Cordova [Cordoba].

Helicina diaphana L. Pfeiffer, 1852

Helicina diaphana L. Pfeiffer, 1852: 98: Honduras (leg. Mr. Dyson, coll. Hugh Cuming)

Type Material: Probable syntype BMNH 196282: Honduras (It was stated at the time of registration that it was possible that some original labeling from the back of the specimen board was not kept. i.e. MC initials and Dyson as collector.)

The assumption of the type status is supported by the fact that Rehder (1966) refers to a photograph of the syntype in the BMNH, probably the specimen was registered when he requested the photograph; the time period would make this seem likely. The specimen (Fig. 188) shows various details of the original description. The operculum is still inside the shell.

Dimensions:

Syntype?: 3.7/4.8/4.9/4.2/2.7/3.0/3.0 mm

Type Locality: "Honduras"

Examined Material

LEG. I. RICHLING

Guanacaste: *N Santa Elena, Sendero at Mirador Gerardo*, 10°22'19"N, 84°48'25"W, 1,450 m a.s.l., 28.07.1999: (IR 855); (IR 856); 14.08.1999: (IR 929); (IR 930); 19.02.2000: (IR 1226); (IR 1228); (IR 1229); 24.02.2001: (IR 1416); (IR 1418); (IR 1419); (IR 1420)

Puntarenas: *Near Monteverde*, about 10°17'24"N, 84°48'04"W, 1 km before entrance on road to reserve, 1,500 m a.s.l.: 26.07.1999: (IR 825); 13.08.1999: (IR 920); (IR 921)

Zona Protectora Arenal-Monteverde: Reserva Biológica Bosque Nuboso Monteverde (about 10°18'08"N, 84°47'41"W, 1,500-1,650 m a.s.l.): 27.07.1999: (IR 844); (IR 845); 18.02.2000: (IR 1196); (IR 1197); 25.02.2001: (IR 1436); *Sendero Bosque Nuboso*: 24.02.1999: (IR 634); (IR 636); *Sendero Roble*: 18.02.1998: (IR 302); *Sendero Chomogo*: 18.02.1998: (IR 296) *About 4 km N Santa Elena, Skywalk*, 10°18'33"N, 84°49'42"W, 1,330 m a.s.l., 27.02.1999: (IR 681)

INBIO COLLECTION

Guanacaste: *Zona Protectora Arenal-Monteverde, Santa Elena: Sendero Encantado*, 10°21'57"N, 84°47'27"W, 1,400 m a.s.l.: leg. Kattia Martinez, 13.07.1994: 4 ads., 6 s.ads., 7 juvs. (INBio 1479270); 3 ads., 6 juvs. (INBio 1479273); *Sendero Encantado*, 10°21'57"N, 84°47'27"W, 1,200 m a.s.l.: leg. Kattia Martinez, 21.06.1996: 3 ads., 3 s.ads., 2 juvs. (INBio 1487482); 2 ads. (INBio 1498545); *Sendero Rancho Alegre*, 10°21'24"N, 84°47'47"W, 1,440 m a.s.l.: leg. Kattia Martinez, 13.11.1994: 2 ads. (INBio 1485425); 1 ad., 1 s.ad. (INBio 1485431)

Zona Protectora Arenal-Monteverde: 1km NE de la casa de información Reserva Santa Elena, 10°21'05"N, 84°47'40"W, 1,550 m a.s.l.: leg. Alexander Alvarado Mendez, 12.01.2000: 3 ads., 2 s.ads. (INBio 3098462); *Sendero Tabacón*, 10°22'55"N, 84°47'40"W, 900 m a.s.l.: leg. Alexander Alvarado Mendez, 03.09.1999: 1 ad. (INBio 1501135)

Alajuela: *Zona Protectora Arenal-Monteverde: Camino a El Valle*, 10°19'44"N, 84°45'55"W, 1,580 m a.s.l.: leg. Kattia Martinez, 20.06.1996: 1 juv. (INBio 1498646); *Estación Alemán*, 10°18'11"N, 84°44'49"W, 940 m a.s.l.: leg. Dunia Garcia, 10.11.1994: 1 s.ad. (INBio 1475971); *Refugio El Valle*, 10°19'04"N, 84°46'41"W, 1,800 m a.s.l.: leg. Kattia Martinez, 11.01.1995: 2 ads., 1 s.ad., 2 juvs. (INBio 1498728)

Zona Protectora Arenal-Monteverde, Sector Peñas Blancas, Estación Alemán, 10°18'09"N, 84°44'52"W: 900 m a.s.l.: leg. Kattia Martinez, 18.08.1994: 1 ad. (INBio 1480178); 1,140 m a.s.l.: leg. Zaidett Barrientos, 10.11.1994: 2 ads., 1 juv. (INBio 1473354); 1 ad. (INBio 1473359)

Zona Protectora Arenal-Monteverde, Reserva Biológica Bosque Nuboso Monteverde: Sendero Pantanoso, 10°18'19"N,

84°47'10"W, 1,620 m a.s.l.: 08.11.1994: 1 s.ad., 1 juv. (INBio 1479473); 15.01.1995: 1 ad., 1 s.ad. (INBio 1498821); 04.04.1995: 1 ad. (INBio 1484024) (all leg. Kattia Martinez); leg. Alejandro Azofeifa, 04.04.1995: 2 juvs. (INBio 1484832)

Cartago: ?Reserva Indígena Chirripó, Zona de captación Río Humo, 09°42'47"N, 83°25'52"W, 1,550 m a.s.l., leg. Zaidett Barrientos, 27.06.1996: 1 ad., 4 s.ad.s, 1 juv. (INBio 1498787)

Puntarenas: Zona Protectora Arenal-Monte Verde, Reserva Biológica Bosque Nuboso Monte Verde: Estación la Casona, 10°18'11"N, 84°47'50"W, 1,600 m a.s.l.: leg. Kattia Martinez, 30.10.1996: 2 ads., 2 juvs. (INBio 1498680); 1 ad., 2 s.ads., 2 juvs. (INBio 1498684); Sendero Bosque Eterno, 10°18'22"N, 84°47'40"W, 1,600 m a.s.l.: 20.01.1995: 1 ad., 1 s.ad. (INBio 1483833); 04.04.1995: 4 ads., 4 s.ads., 1 juv. (INBio 1485231); 04.07.1995: 3 ads. (INBio 1485229); 19.06.1996: 1 ad. (INBio 1498693) (all leg. Kattia Martinez); Sendero

Bosque Nuboso, 10°17'59"N, 84°47'36"W, 1,600 m a.s.l.: 14.06.1994: 2 ads. (INBio 1466785); 16.07.1994: 1 ad., 1 s.ad. (INBio 1479239); 1 s.ad. (INBio 1479860); 16.09.1994: 2 ads., 1 s.ad. (INBio 1480117); 14.01.1995: 3 ads., 1 s.ad. (INBio 1498583); 22.06.1996: 2 ads., 1 juv. (INBio 1498519) (all leg. Kattia Martinez); Sendero Bosque Nuboso, 10°17'59"N, 84°47'36"W, 1,520 m a.s.l.: leg. Zaidett Barrientos, 14.10.1994: 1 ad., 1 juv. (INBio 1468138); 1 ad. (INBio 1468209); Sendero Bosque Nuboso, 10°17'59"N, 84°47'43"W, 1,520 m a.s.l.: leg. Alexander Alvarado Mendez, 03.02.1999: 1 ad. (INBio 1501428); Sendero Chomogo, 10°18'22"N, 84°47'23"W, 1,690 m a.s.l.: leg. Kattia Martinez, 13.08.1994: 1 ad. (INBio 1480143); 1 juv. (INBio 1480156); Sendero Chomogo, 10°18'22"N, 84°47'23"W, 1,640 m a.s.l.: 10.10.1994: 1 ad., 2 s.ads., 1 juv. (INBio 1485418); 25.11.1995: 1 ad. (INBio 1498708); 18.02.1997: 1 ad. (INBio 1498840) (all leg. Kattia Martinez); Sendero el Río, 10°18'29"N, 84°47'37"W, 1,600 m



FIGS. 189, 190. *Helicina monte verdensis* n. sp. FIG. 189. Holotype, INBio 3542627, height 6.6 mm. FIG. 190. Paratype 2, ZMB 103884, height 6.8 mm; scale bar 2.5 mm.

a.s.l.: 04.04.1995: 1 ad., 1 s.ad. (INBio 1484664); 04.07.1995: 1 ad., 1 s.ad. (INBio 1484659) (both leg. Alejandro Azofeifa); 15.07.1994: 1 s.ad. (INBio 1480137); 1 s.ad. (INBio 1480151); 16.09.1994: 2 s.ad. (INBio 1480122); 08.12.1994: 2 juvs. (INBio 1480142); 04.07.1995: 6 ads. (INBio 1485230); 29.10.1996: 1 ad. (INBio 1498835) (all leg. Kattia Martinez); *Sendero el Roble*, 10°18'16"N, 84°47'27"W, 1,600 m a.s.l.: leg. Kattia Martinez, 08.11.1994: 1 ad. (INBio 1479363); *Sendero el Camino*, 10°18'03"N, 84°47'15"W, 1,560 m a.s.l.: 23.05.1994: 2 ads. (INBio 1466975); 14.07.1994: 1 s.ad. (INBio 1479374); 1 ad. (INBio 1480153); 13.12.1994: 1 ad., 1 s.ad. (INBio 1484678) (all leg. Kattia Martinez)

OTHER SOURCES

COSTA RICA

Guanacaste: 6 mi NNE Tilaran, on road to Arenal [about 10°33'N, 84°59'W?], 17.07.1971: 1 ad. (UF 69855)

San José: Alata la Palma [Alto Palma?, about 10°03'N, 84°00'W], 07.08.1971: 1 s.ad. (UF 69856)

Description

Shell (Figs. 189, 190, 336I–J): Conical, thin and fragile, medium to small sized, semitransparent, shiny. Color: whorls unicolored, whitish-opaque, yellowish to bright yellow or even brownish; apical whorls sometimes with a crimson spot. Surface textured with fine and regular growth lines (Fig. 192), causing the glossy appearance. Embryonic shell with about 1 whorl; $3\frac{3}{8}$ –4) subsequent whorls convex; last whorl very evenly rounded at the periphery; whorls equally extending in size or last whorl even more rapidly increasing in diameter, forming a pointed spire. Suture moderately impressed. Aperture oblique and curved backwards; last whorl slightly more descending towards aperture and inserting below periphery. Outer lip independently from the color of the whorls always whitish-opaque, slightly thickened and very narrowly expanded and reflexed. Transition to columella continuous with a slight notch. Columella slightly curved, transition to the body whorl without any groove. Basal callus very weakly developed and slightly granulated.

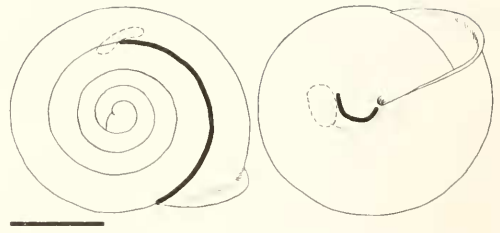


FIG. 191. Axial cleft and muscle attachments of *Helicina monteverdensis* n. sp., INBio 3542627 (holotype); scale bar 2.5 mm.

Internal Shell Structures: (Fig. 191)

Teleoconch Surface Structure (Fig. 192): The surface structure is similar to that of *Helicina gemma*.

Embryonic Shell: Among the specimens studied from the populations of Monteverde and Mirador Gerardo, the embryonic shells show large deviations in structure, showing all intermediary variations in pit size from pronounced pits as in *Helicina gemma* to small ones as in *H. beatrix* (Fig. 193A, B). For comparison with *H. fragilis*, a Guatemalan specimen was studied (Fig. 194), but due to the high variations in *H. monteverdensis* n. sp., structural differences cannot be codified. By the way of contrast, the size differs remarkably: the type lot and

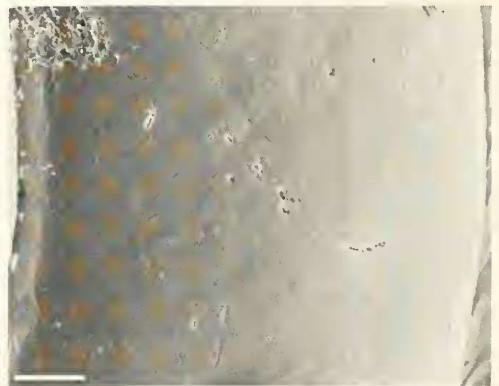


FIG. 192. Teleoconch surface structure of *Helicina monteverdensis* n. sp., 2nd whorl; scale bar 100 µm.

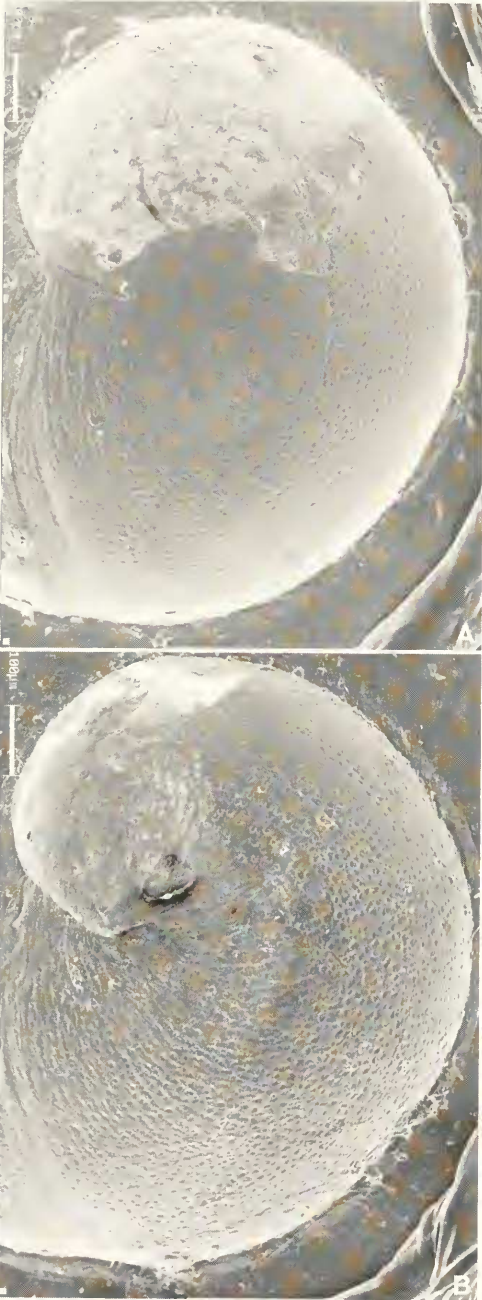


FIG. 193. Embryonic shell of *Helicina monteverdensis* n. sp. A. Mirador Gerardo, IR 1226. B. Same data; scale bar 100 μm .

other Guatemalan specimens show a range of 580 to 760 μm , whereas the embryonic shell of the Costa Rican specimens of *H. monteverdensis* n. sp. is clearly larger (830 to 1,000 μm). These differences clearly exceed the possible deviations caused by effects of altitude, at least as far as the results for *H. gemma* suggest. Furthermore, the specimens from UF 189883 with a small embryonic shell size also originate from an altitude of 1,300 m. The same is true for the type lot of *H. meridigera*, the embryonic shell of which is also remarkably smaller.

The smaller specimens from the population of Mirador Gerardo possess somewhat smaller embryonic shells on the average. The relation of embryonic shell size to the shell size is discussed below.

Diameter: 935 μm (± 25) (900–1,000) ($n = 21$) (IR 634, IR 844, Monteverde); 897 μm (± 29) (830–990) ($n = 15$) (IR 1226, Mirador Gerardo); 708 μm (± 44) (620–760) ($n = 4$) (BMNH 1893.2.4.809–812, type lot of *Helicina fragilis*, lectotype: 620 μm); 610 μm



FIG. 194. Embryonic shell of *Helicina fragilis*; scale bar 100 μm .

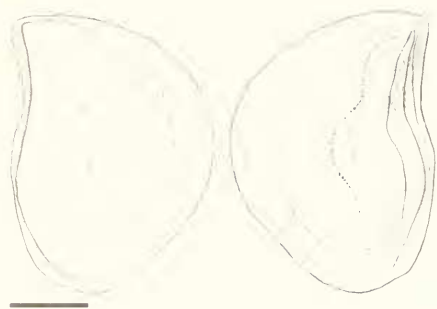


FIG. 195. Operculum of *Helicina monteverdensis* n. sp., INBio 3542627; scale bar 1 mm.

(UF 190045: Guatemala: Alta Verapaz Department, 9 km W of Lanquin, 15°35'03"N, 90°03'20"W, 690 m a.s.l., leg. F.G. Thompson et al.); 620 μm (± 20) (600–640) ($n = 2$) (UF 189883: Guatemala, Alta Verapaz Department, 1.5 km SE of (San Juan) Chamelco, 15°24'20"N, 90°18'28"W, 1,300 m a.s.l., leg. F.G. Thompson); 608 μm (± 18) (580–630) ($n = 5$) (UF 237423: Guatemala: Chama, leg. A.A. Hinkley, ex coll. Beal-Maltbie); 650 μm (± 0) (650) ($n = 2$) (BMNH 20010725.1–2, type lot of *Helicina merdigera*).

Operculum (Fig. 195): Very slightly calcified, calcareous plate covering only part of the outer surface, thickened towards the columellar side. Color whitish-yellow to pale horny-amber, nearly transparent throughout. Columellar side slightly S-shaped, upper end acute and pointed, lower end rounded and continuously changing into outer margin.

Animal (Fig. 338F, G): The color resembles that of *Helicina gemma*, but varies more strongly. In the individuals originating from Monteverde, the head-foot is usually much paler, only the tentacles are tinged grey; in the mantle pigmentation, the whitish-yellow part is very prominent, but the dark spots very often form an irregular band at the periphery. The pattern in specimens from Mirador Gerardo more closely resembles that of *H. gemma*, but it ranges from nearly black individuals with some very small yellowish-white spots to the reverse, with few slender black lines and spots. In this population, a distinct dark band has never been observed. Usually the dark part of the head-

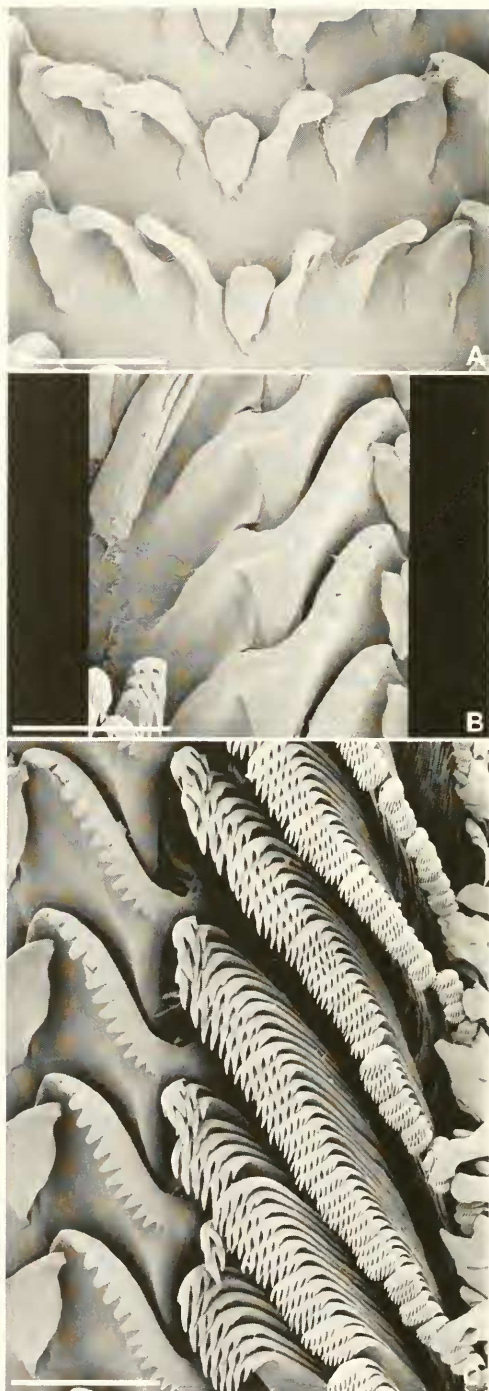
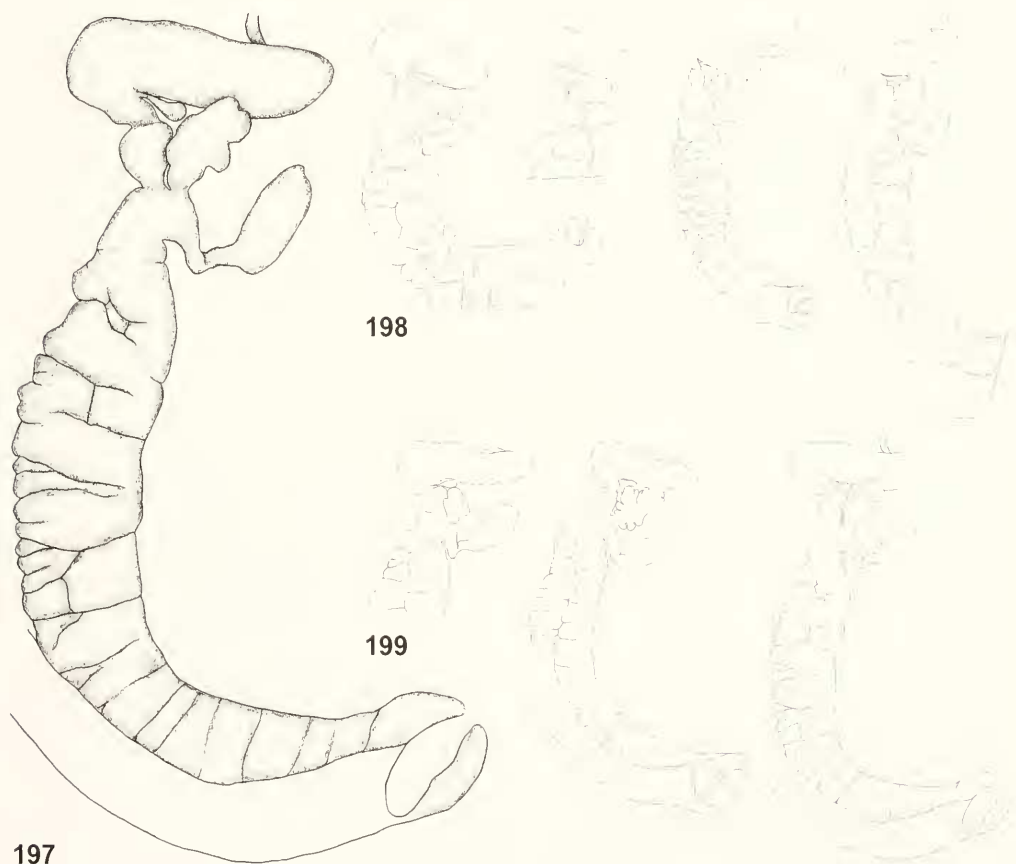


FIG. 196. Radula of *Helicina monteverdensis* n. sp. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 μm .

foot is larger and more intensive in specimens with a darker mantle pigmentation. These considerable variations within a population seem to be typical. The few specimens from the Cartago Province are either dark or pale. The mantle pigmentation is clearly visible through the thin shell.

Radula (Fig. 196): All centrals lack well defined cusps. Comb-lateral with 8 cusps, only one exception with 11 or 13 cusps on the other side respectively (Fig. 196C). Cusps on marginals rapidly increasing in number. Radula with about 46–73 rows of teeth.

Female Reproductive System (Figs. 197–199): The reproductive tract of *Helicina monteverdensis* n. sp. is similar to that of *H. gemma* and equal in size and proportions except for the bursa copulatrix. The latter seems to be consistently smaller, although specimens collected during both (dry and rainy) seasons were studied in either species to exclude possible physiological changes. Furthermore, the shape of the bursa copulatrix varies more in *H. monteverdensis* n. sp. Lobes are not always distinctly developed and they are less regular.



FIGS. 197–199. *Helicina monteverdensis* n. sp. FIG. 197. Female reproductive system, IR 844. FIG. 198. Variability of the female reproductive system, population from Mirador Gerardo, IR 1226. FIG. 199. Variability of the female reproductive system, population from Monteverde, IR 844; scale bar 1 mm (Fig. 197), 2 mm (Fig. 198–199).

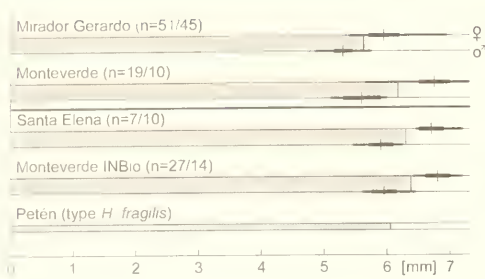


FIG. 200. Shell height of different populations of *Helicina montevertensis* n. sp. in Costa Rica according to Table 11; on each line: mean value, standard deviation, absolute range; number of individuals given as “n = females/males”; upper line: females, lower line: males; in between and shaded: average of both for comparison with populations of unknown sex; sex of individuals from Santa Elena and Monteverde INBio not determined anatomically (see text).

Morphometry and Sexual Dimorphism (Table 11, Figs. 200–205)

Around the type locality, the species was collected in favorable numbers for the morphometric analysis. Three localities are differentiated from N to S: Mirador Gerardo at the beginning of the northern slope of the Cordillera de Tilarán, the Santa Elena reserve and finally samples mainly in and around the Reserva Biológica Bosque Nuboso Monteverde. The latter are separated in the lots that were anatomically investigated (coll. IR) and INBio’s. Both populations included from the latter collection (Figs. 200–204, be-

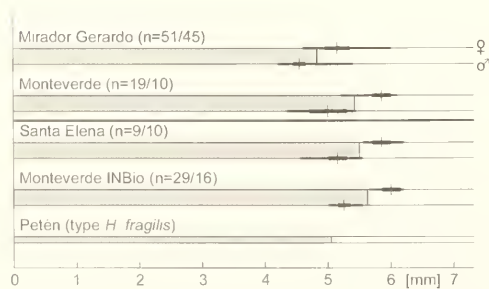


FIG. 201. Minor diameter of shell of different populations of *Helicina montevertensis* n. sp. in Costa Rica according to Table 11; for explanations see Fig. 200.

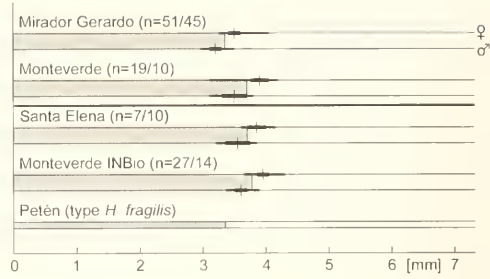


FIG. 202. Expansion of outer lip of different populations of *Helicina montevertensis* n. sp. in Costa Rica according to Table 11; for explanations see Fig. 200.

low thick line), which could not be analyzed for their sex, were separated, as in *Helicina beatrix*, to avoid the artificial high deviations of measurements with mixed sexes. For comparison in the discussion, the lectotype of *H. fragilis* is included in the figures.

Morphometry: The shells of the population “Mirador Gerardo” are remarkably smaller in all measurements than the other populations, which are similar to each other. The constant pattern of differences of the populations for the different measurements suggests the same shape of the shell. In comparison with *Helicina gemma* closely resembling the species, it is remarkable that only the populations with the biggest shells (“Finca Montaña Grande”, “Cerro Cocori”) attain the size of the new species from Monteverde, whereas in the closer population “Mirador Gerardo”, the average shell

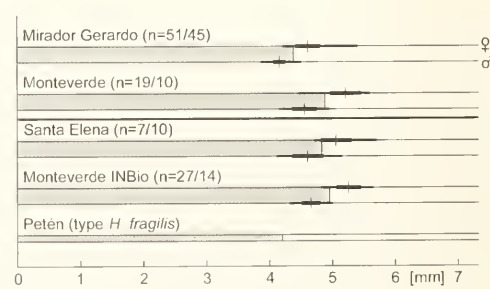


FIG. 203. Height of last whorl of different populations of *Helicina montevertensis* n. sp. in Costa Rica according to Table 11; for explanations see Fig. 200.

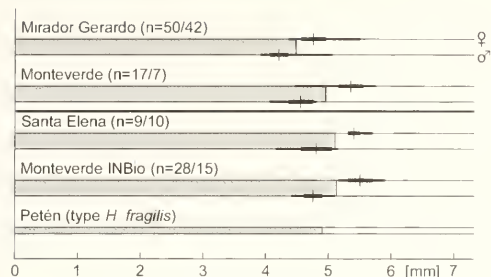


FIG. 204. Height of columellar axis of different populations of *Helicina monteverdensis* n. sp. in Costa Rica according to Table 11; for explanations see Fig. 200.

size is clearly smaller than in all *H. gemma* populations. Thus, *H. monteverdensis* n. sp. displays greater differences in size in just a few closely located and ecological similar populations than does the comparatively widespread *H. gemma* in the several populations investigated. This observation supports the distinctness of the two species.

Sexual Dimorphism: In both populations, the females possess bigger shells. The data overlap only very slightly with the measurements of the males, possibly because of the comparatively high number of specimens included, rendering individual high deviations more likely. The separation of both sexes is additionally shown for the original set of data of height and minor diameter for the population "Monteverde" and "Mirador Gerardo" (Figs. 206–207). In volume, the males only amount to $\frac{2}{3}$ or less than the females. The differences displayed for the populations are very constant for each measurement. As explained in *H. beatrix*, the well-developed sexual dimorphism allows a

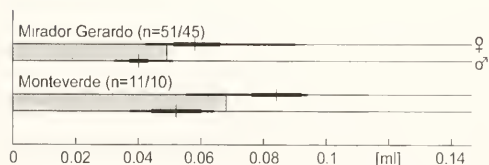


FIG. 205. Shell volume of different populations of *Helicina monteverdensis* n. sp. in Costa Rica according to Table 11; for explanations see Fig. 200.

separation of sets of mixed data (illustrated for Monteverde INBio, Fig. 208).

Habitat

Helicina monteverdensis n. sp. has been observed crawling and aestivating on leaves of several small-leaved plants of the undergrowth. Especially at Mirador Gerardo where Heliconiaceae are abundant on the forest margins, it was mainly found on older leaves of plants that were covered with moss and algae. During rainy and cloudy weather, it crawls on both the upper and lower side of the leaves. It has not been seen in leaf litter. In Monteverde and adjacent areas, the species occurs sympatrically with *H. funcki* and *Alcadia hojargasca*.

Distribution (Fig. 209)

Helicina monteverdensis n. sp. seems to be adapted to higher altitudes, most records around 1,500 m. A single exception is the site north of Tilarán (about 700 m?), which can also be located south of or today within the reservoir, because it was collected before the construction of the Embalse de Arenal reservoir. The species occurs in the Cordillera de Tilarán and the Cordillera Central. It is well distributed in the cloud forests of the area of Monteverde – Santa Elena. The record from the northeastern slopes of the Cordillera Talamanca is only tentatively attributed to the new species; further material is required. As the record from the Cordillera Central indicates, the species is probably much more widespread, but many possible sites have either been poorly investigated or not at all. Except for the Cordillera de Guanacaste, *H. monteverdensis* n. sp. replaces *H. gemma* at higher altitudes.

Discussion

The population in Monteverde consists of brightly yellow to whitish shelled specimens, whereas individuals from the Mirador Gerardo within a very limited collection area exhibit a wider range of color, additionally including brownish specimens. The outer lip is always whitish.

Helicina monteverdensis n. sp. most closely resembles *H. gemma* from which it differs by the constantly different color of the outer lip and adjacent part of the last whorl. Besides

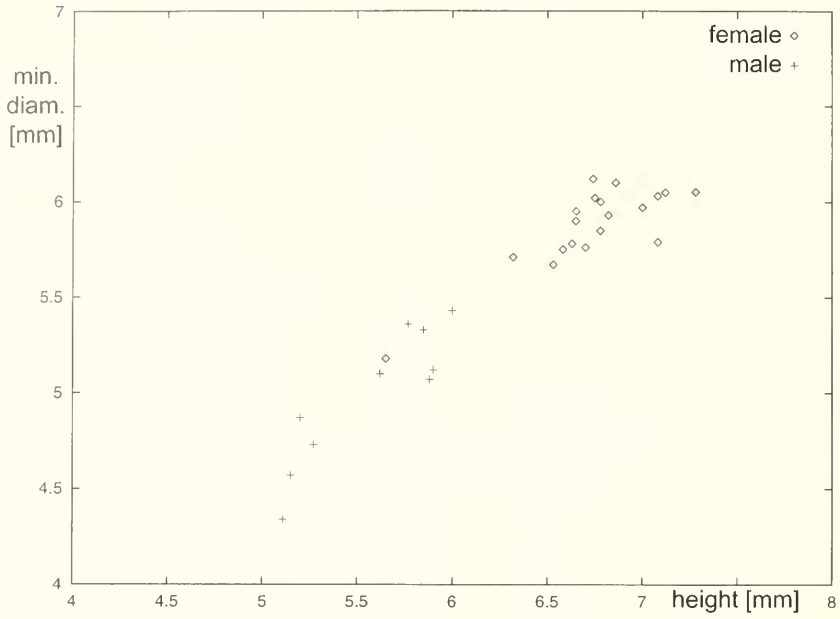


FIG. 206. Range of measurements in females and males of *Helicina monteverdensis* n. sp. exemplary for height and minor diameter in the population from Monteverde.

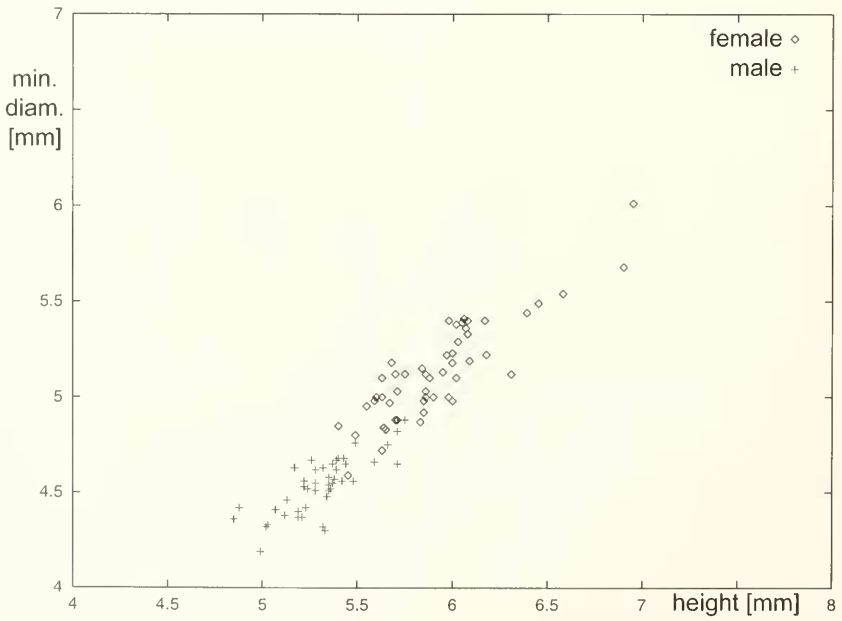


FIG. 207. Range of measurements in females and males of *Helicina monteverdensis* n. sp. exemplary for height and minor diameter in the population from Mirador Gerardo.

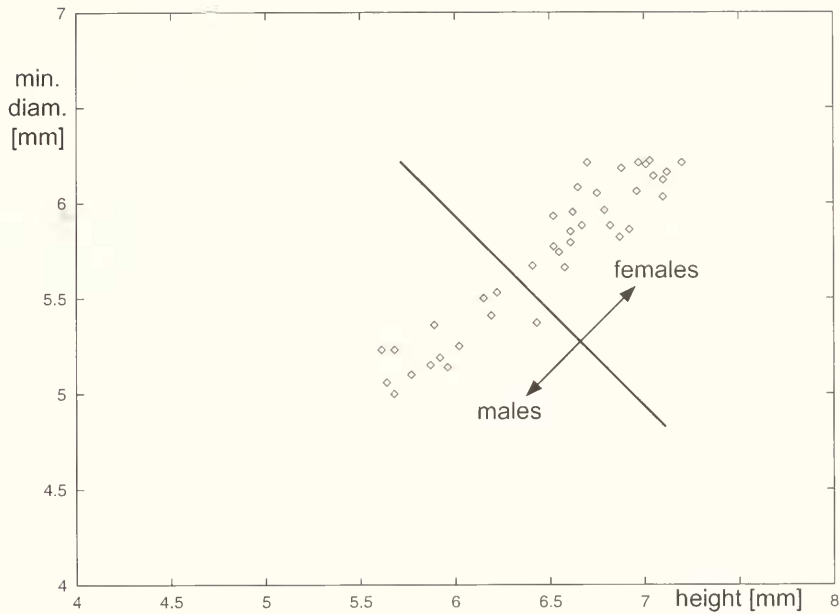


FIG. 208. Plot of measurements for height and minor diameter for individuals of *Helicina monteverdensis* n. sp. of unknown sex, exemplary for the population of Monteverde INBio and the separation proposed.

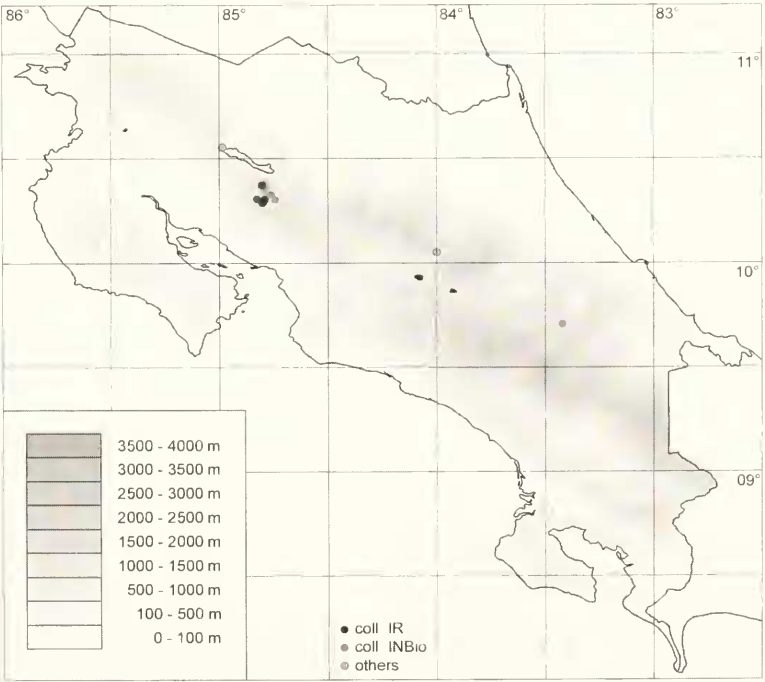


FIG. 209. Records of *Helicina monteverdensis* n. sp. in Costa Rica.

TABLE 11. Measurements of different populations of *Helicina monteverdensis* n. sp. given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens; sex of individuals from Santa Elena and Monteverde INBio not determined anatomically (see text) (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

"Mirador Gerardo" (altitude 1450 m) lots IR 929, IR 1416							"Monteverde" (altitude 1500–650 m) lots IR 296, 634, 825, IR 844, IR 1196				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	5.93	0.24	5.40	6.95	51	6.74	0.23	5.65	7.28	19
Height	m	5.31	0.15	4.85	5.75	45	5.58	0.31	5.11	6.00	10
Maj. diam.	f	5.56	0.23	4.93	6.48	51	6.32	0.17	5.61	6.62	19
Maj. diam.	m	4.96	0.14	4.45	5.41	45	5.46	0.34	4.82	6.02	10
Min. diam.	f	5.14	0.20	4.59	6.01	51	5.87	0.16	5.18	6.12	19
Min. diam.	m	4.54	0.12	4.19	4.88	45	4.99	0.29	4.34	5.43	10
Outer lip	f	3.50	0.11	3.25	4.06	51	3.91	0.15	3.60	4.18	19
Outer lip	m	3.21	0.10	2.95	3.52	45	3.48	0.20	3.10	3.80	10
Last whorl	f	4.62	0.18	4.18	5.40	51	5.22	0.23	4.47	5.58	19
Last whorl	m	4.17	0.12	3.85	4.52	45	4.54	0.21	4.16	4.95	10
Col. axis	f	4.75	0.20	4.37	5.52	50	5.33	0.20	4.45	5.75	17
Col. axis	m	4.22	0.13	3.89	4.57	42	4.56	0.19	4.03	4.80	7
Weight	f	0.013	0.002	0.009	0.022	51	0.016	0.002	0.011	0.019	11
Weight	m	0.011	0.002	0.007	0.017	45	0.013	0.002	0.008	0.018	10
Volume	f	0.058	0.007	0.042	0.090	51	0.084	0.008	0.055	0.094	11
Volume	m	0.040	0.003	0.032	0.051	45	0.052	0.008	0.037	0.064	10

"Monteverde INBio" (altitude 1520–1690 m)
lots INBio 1466785, 1466975, 1468138,
1468209, 1479239, 1479363, 1480117,
1480143, 1480153, 1483833, 1484024,
1484659, 1484664, 1484678, 1485229,
1485230, 1485231, 1485418, 1498519,
1498583, 1498680, 1498684, 1498693,
1498708, 1498821, 1498835, 1498840,
1501428

"Santa Elena" (altitude 1200–1550 m)
lots INBio 1479270, 1479273, 1485425,
1485431, 1487482, 1498545, 3098462

	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	6.72	0.19	6.46	7.21	7	6.82	0.20	6.41	7.20	27
Height	m	5.90	0.21	5.43	6.25	10	5.93	0.20	5.61	6.43	14
Maj. diam.	f	6.29	0.17	5.92	6.63	8	6.42	0.19	5.97	6.78	29
Maj. diam.	m	5.58	0.20	5.01	5.99	10	5.70	0.16	5.43	6.10	16
Min. diam.	f	5.84	0.13	5.55	6.19	9	5.99	0.15	5.66	6.22	29
Min. diam.	m	5.13	0.17	4.53	5.56	10	5.25	0.12	5.00	5.53	16
Outer lip	f	3.83	0.16	3.58	4.17	7	3.95	0.12	3.65	4.30	27
Outer lip	m	3.56	0.18	3.18	3.85	10	3.60	0.11	3.33	3.91	14
Last whorl	f	5.07	0.24	4.70	5.70	7	5.24	0.19	4.80	5.66	27
Last whorl	m	4.61	0.23	4.12	5.13	10	4.66	0.14	4.32	5.00	14
Col. axis	f	5.42	0.10	5.29	5.68	9	5.51	0.19	5.13	5.89	28
Col. axis	m	4.79	0.23	4.13	5.15	10	4.77	0.15	4.41	5.08	15

morphometric differences discussed above, the whorls of *H. montevertensis* n. sp. appear more inflated. The high variation in body color of *H. montevertensis* n. sp. has not been observed in other species.

Small, thin-shelled, yellowish-whitish-transparent Helicinidae without spiral striations from Central America (mainly Mexico and Guatemala) were normally referred to *Helicina fragilis* or its subspecies *H. fragilis elata* with the synonyms *Helicina merdigera* and the dubious *Helicina mohriana* (e.g., Fischer & Crosse, 1880–1902; von Martens, 1890–1901; Baker, 1922a, 1928). Wagner (1908) did just this when he studied such specimens in the collection of the ZMB from the more southern parts of Costa Rica. Those specimens from the Valle de Talamanca and the neighboring Valle de Estrella were reinvestigated and partly belong to *H. escondida* n. sp., *H. chiquitica* or partly remain dubious in their identification (see under *H. chiquitica*).

To clarify the classification of the small, fragile, whitish Helicinidae from the Monteverde area, the type material of the taxa mentioned above and many lots from Mexico, Guatemala, Honduras and Belize were studied, mainly in the collection of the UF.

Helicina fragilis differs from *H. montevertensis* n. sp. in having fewer whorls and a much smaller embryonic shell, although the general size of the shells is about the same. The aperture and last whorl is relatively lower, the spire higher. Furthermore, in many specimens of *H. fragilis*, a slight angulation at the periphery (stronger in juvenile stage) is maintained to at least the beginning of the last whorl (e.g., paralectotypes), which in *H. montevertensis* n. sp. is always rounded. The types were collected under decaying leaves, whereas the new species is arboreal. Baker (1928) observed *H. fragilis elata* on rock ledges, weeds and low brush, but assumed the aestivation on the ground.

The lectotype of *Helicina merdigera* is slightly angulated at the periphery throughout the last whorl, which is a little shouldered below the suture. In comparison with *H. fragilis* and the new species, the shell surface is more roughly sculptured with irregular growth lines and oblique grooves, the outer lip is less reflexed and the thickening is shifted a little inwards. The lower part of the aperture protrudes further, forming a nearly rectangular edge at the transition to the columella, whereas in *H. fragilis* and *H. montevertensis*

n. sp., the transition is continuously or even with a little notch. Other features are similar to *H. fragilis* providing additionally evidence for the distinctness from the new species. Fischer & Crosse (1893) related the observation by Sallé that *H. merdigera* covers its shells with own excrement. It is interesting to note that the fragmented paralectotype shows traces of exactly such encrustation on the shell pieces. If this behavior turns out to be typical for *H. merdigera*, it is also in contradiction to the behavior of the Costa Rican specimens which were never observed to have agglutinated anything on their shiny shells. Considering the differences in the type material, it seems more appropriate to treat *H. merdigera* as specifically distinct from *H. fragilis* until more material is carefully studied, but this is beyond the focus of the current study.

Von Martens (1890), having compared Shuttleworth's typical specimen of *Helicina elata* to a Guatemalan sample, only recognized the smaller size and a more slender peristome. Besides size the syntype at hand differs in a more globose shell, that is, a less elevated spire with a blunt apex, the lower whorls increasing less in diameter. In this respect, it also differs from *H. montevertensis* n. sp. The figure in Fischer & Crosse (1893) does not match the syntype at all. As described by Shuttleworth and pointed out by Von Martens (1890), *H. elata* exhibits a dentiform prominence at the base of the columella (like *H. merdigera*), which is lacking in the new species. Whether or not *H. elata* has to be treated as a subspecies of *H. fragilis* is a question beyond the scope of this study.

Type material of *Helicina mohriana* could not be located. L. Pfeiffer probably kept it in his own collection, which became part of the collection of Dohrn (Dance, 1986). The latter is said to have been destroyed in the Museum Stettin, Poland, during World War II (Clench & Jacobson, 1971). Wagner (1908) depicted the species for the first time (*Alcadia* (*Leialcadia*) *fragilis mohriana*), but the source of his material is unknown, and the one of two specimens (Wagner, 1908: pl. 14, figs. 14–16) originating from the type locality, Orizaba, represent a not yet fully grown shell. Because he does not give any explanation for this identification and completely ignored "*merdigera*" and "*elata*", it does not contribute to the clarification of the taxon. Thus, it obviously remains a dubious species, which however is differentiated from *H. montevertensis* n. sp. by a groove in the

umbilical area near the columella mentioned in the original description ("juxta columellam brevem excavatus").

Another dubious species (von Martens, 1891) of this complex is *Helicina diaphana* from Honduras. It has only been depicted very inadequately in Reeve (1874), and it completely escaped the attention of Fischer & Crosse (1880–1902) and Wagner (1907–1911). Rehder (1966) stressed the specific dissimilarity to *Helicina boucourti* Crosse & Fischer, 1869, rendering it more likely to a closer affinity with the "small, thin, fragile, whitish species". The study of the probable syntype shows, on one hand, that *H. diaphana* is clearly different from *H. montevertensis* n. sp., but, on the other hand, that the taxon does not deserve to be treated as a dubious species, because the description was not based on a juvenile shell. *H. diaphana* is broader than high, appearing depressed, but the periphery is only very roundly angulated, if at all. The suture is very weakly impressed, the apex blunt. The uppermost $\frac{1}{4}$ whorls of the teleoconch bear widely spaced spiral ridges, subsequently the shell is sculptured with irregular growth lines and an ornamentation of small oblique grooves. The aperture is oblique, inserting below the periphery, the outer lip developed, but only slightly expanded and reflexed. The transition to the columella lacks a notch or denticle.

Considering also *H. chiquitica* and *H. escondida* n. sp., it appears that the Mexican and Guatemalan taxa discussed are not distributed as far southwards as previously assumed.

The original material of the records of Monge-Nájera (1997) for *H. oweniana* and *H. beatrix* was checked in the collection of INBio and can partially be attributed to *H. montevertensis* n. sp. For differences to these species, compare also the closely related *H. gemma*.

***Helicina* ("Gemma") *escondida*
Richling, n. sp.**

Type Material

Holotype: INBio 3542623, female (leg. I. Richling, 12.03.2001, ex IR 1543)
Paratype 1: INBio 3542624, male (same data as holotype)
Paratype 2: ZMB 103880, female (same data as holotype)
Paratype 3: ZMB 103881, female (same data as holotype)

Dimensions:

Holotype: 6.2/6.0/6.4/5.4/3.8/4.9/5.0 mm
Paratype 1: 5.9/5.6/6.1/5.1/3.6/4.6/4.5 mm
Paratype 2: 6.8/6.1/6.6/5.7/3.8/5.1/5.3 mm
Paratype 3: 6.6/5.9/6.4/5.5/3.7/4.9/5.3 mm

Type Locality

SE-Costa Rica, Limón Province, approximately 9 km W of Matina, a little upstream on the Río Barbilla from the crossing of the road from Siquirres to Limón, along a tributary of Río Barbilla, 10°03'29"N, 83°22'24"W, 70 m a.s.l., valley of small creek in rain forest (probably secondary forest)

Material Examined

LEG. I. RICHLING

Heredia: S Puerto Viejo de Sarapiquí, *Zona Protectora La Selva*, near OTS-Station, about 10°25'53"N, 84°00'18"W, 60 m a.s.l., 05.09.1999: (IR 1056)

Limón: About 9 km W of Matina, road Limón to Siquirres, a little stream up the *Río Barbilla*, along a tributary of Río Barbilla, in the valley of a small creek in rain forest, 10°03'29"N, 83°22'24"W, 70 m a.s.l., 12.03.2001: (IR 1543)

N Shiroles, Cerro Mirador, along trail, 09°36'37"N, 82°57'43"W, 430 m a.s.l.: 16.03.2001: (IR 1601)

INBIO COLLECTION

Limón: *Sector Hitoy Cerere*: Sendero Bobócara, 09°40'31"N, 83°00'31"W, 200 m a.s.l., leg. malacological staff of INBio, 10.01.1993: 1 ad. (INBio 1466441); 400 m NE de la Estación de Hitoy Cerere, Sendero la "Finca", 09°40'36"N, 83°01'26"W, 110 m a.s.l., leg. Alexander Alvarado Mendez, 27.09.2000: 1 ad. (INBio 3091794)

Reserva Biológica Hitoy Cerere: Cruce entre Sendero Revienta Pechos y Sendero Espavel, 09°39'12"N, 83°00'58"W, 600 m a.s.l.: leg. Alexander Alvarado Mendez, 24.04.1999: 5 ads. (INBio 1497850); *Sendero Bobócara*: 09°40'02"N, 83°02'42"W, 500 m a.s.l., 12.06.1999: 1 ad., 1 s.ad. (INBio 3091132); 09°40'53"N, 83°04'09"W, 798 m a.s.l., 17.06.1999: 6 ads., 1 s.ad., 1 juv. (INBio 3542523) (all leg. Alexander Alvarado Mendez)

Reserva Indígena Tayni, Sendero Bobócara, 09°40'28"N, 83°02'12"W, 200 m a.s.l., leg. Alexander Alvarado Mendez, 15.07.1999: 1 ad. (INBio 1498244)

OTHER SOURCES

COSTA RICA

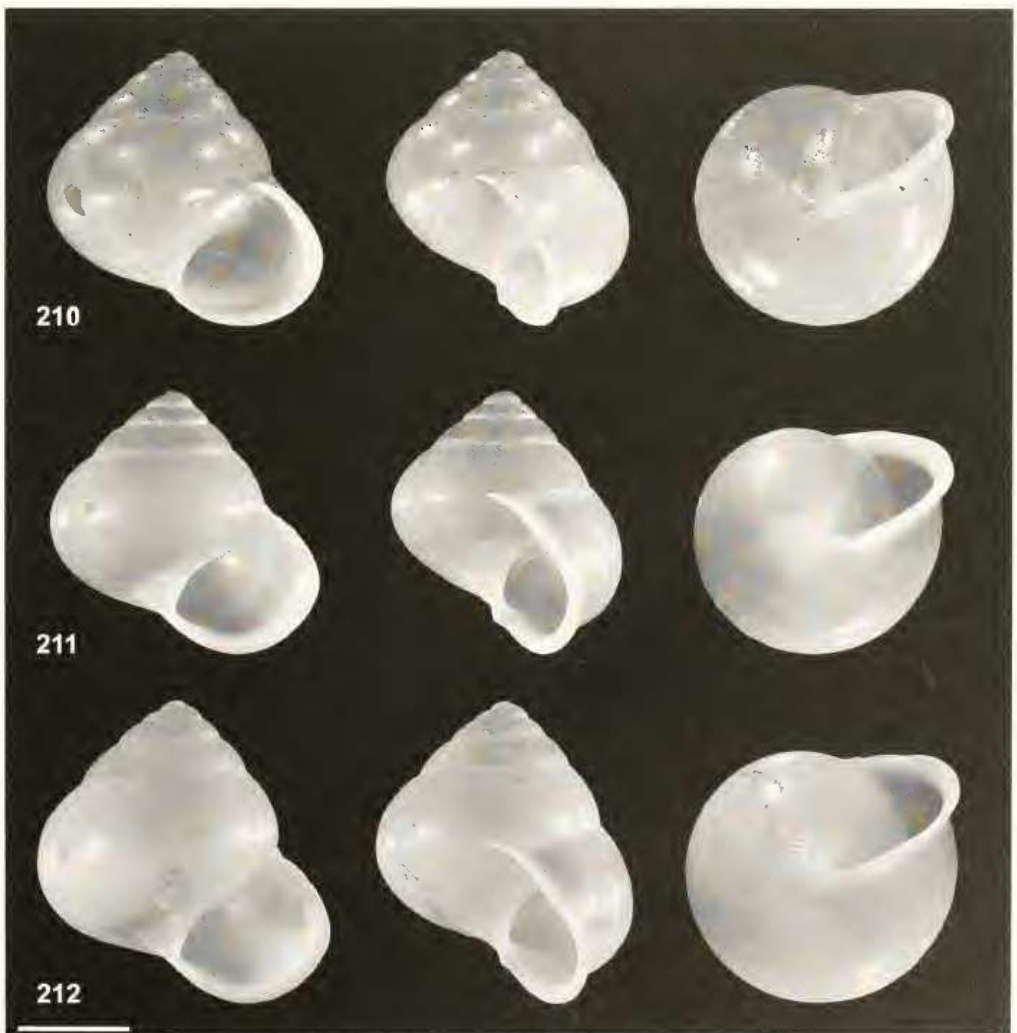
Limón: Los Diamantas Farm [about 10°11'N, 83°37'W], 11.08.1971: 1 ad. (UF 69847); determination uncertain: Los Diamantes Farm, 12 mi SE Guapiles [about 10°11'N, 83°37'W], leg. R.W. McDiarmid, 13.08.1971: 1 s.ad. (UF 217530)

Road cut, along S bank of Río Banano, opposite La Bomba, 09°54'49.7"N, 83°03'56.4"W, leg. D.G. Robinson & J.M. Montoya (Stn. 98 CR-15), 21.09.1998: 2 ads. (APHIS PPQ USDA)

Talamanca, Río Estrella [about 09°43'N, 83°00'W], leg. Pittier (ZMB 103249); Valle del Río Estrella, Talamanca [about 09°43'N, 83°00'W], leg. H. Pittier, III.95 (ZMB 48235) Valleé de Brabri, Talamanca [Bratsi? about 09°33'40"N, 82°53'28"W], leg. H. Pittier, VIII.98 (ZMB 103248)

Cartago: Turrialba [about 09°54'30"N, 83°41'W], International American Agricultural Institute, 2000 ft., leg. F.G. Thompson (FGT-76), 03.08.1963: 2 ads. (UF 214143)

Costa Rica, without locality specified: ex Sowerby & Fulton: 1 ad. (UF 243507: 1 of 3 spec.)



FIGS. 210–212. *Helicina escondida* n. sp. FIG. 210. Holotype, INBio 3542623, height 6.2 mm. FIG. 211. Paratype 1, INBio 3542624, height 5.9 mm. FIG. 212. Paratype 2, ZMB 103880, height 6.8 mm; scale bar 2.5 mm.

Etymology

The name represents two aspects of the species: for a long time it has escaped scientific recognition, its occurrence is very "hidden" in natural environments, and the small size and variations of the color render it difficult to find. I had been searching all day without success until I came across some tiny helicínids, which turned out to represent two new species: *chiquitica* and "escondida" (Spanish) = "hidden". The Spanish word is preferred here in homage to its origin and because the Latin translations are occupied by other helicínid species.

Description

Shell (Figs. 210–212, 336K–M): conical, small, fragile and slightly dull. Color: unicolored yellow except for the outer lip and a slight, very thin yellowish-white band directly under suture. Embryonic shell about 1 whorl; $4\frac{1}{8}$ ($3\frac{7}{8}$ – $4\frac{5}{8}$) subsequent whorls equally extending in size; last whorl rounded at periphery; only slightly convex, giving the spire a very regular and straight appearance. Periostracum thin, under magnification with very fine equally spaced spiral striations at the periphery (up to about 9 lines) and a texture of fine oblique lines that makes it appear dull. Aperture oblique and very straight. Outer lip independently from color of whorls always yellowish-white, slightly thickened and reflexed nearly rectangularly to the whorls; transition to columella only with a very little denticle. Basal callus very weakly developed, umbilical area finely granulated with a little groove parallel to the columella.

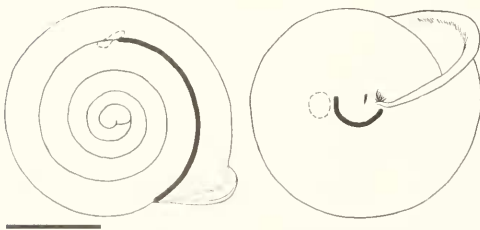


FIG. 213. Axial cleft and muscle attachments of *Helicina escondida* n. sp., INBio 3542623; scale bar 2.5 mm.

Internal Shell Structures (Fig. 213):

Teleoconch Surface Structure: The transitional pattern (Fig. 214A, B) stretches for nearly $\frac{3}{4}$ of a whorl, the following structure of oblique diverging grooves is only weakly developed, becoming still weaker during growth (Fig. 214C, D), but not disappearing. Furthermore, the surface is sculptured with periostracal spiral ridges that begin in the second whorl.

Embryonic Shell (Fig. 215): Except for size, the embryonic shell closely resembles that of *Helicina funcki*. In the specimens under study, it shows only minor deviations, for example, the lines of pits starting somewhat later.

Diameter: 728 μm (± 25) (680–780) ($n = 19$) (IR 1543).

Operculum (Fig. 216): Thin and only slightly calcified. Color yellowish and transparent. Columellar margin slightly S-shaped, upper end acute, lower end only weakly angulated, rounded. Inner surface with a little ridge parallel to the columellar margin.

Animal (Figs. 338H, 339A–B): The color of the soft body is variable. The foot is light whitish-yellow and becoming brownish-grey upwards. Dorsal anterior and posterior end and tentacles being darkest, but some individuals are much lighter than other. The mantle color varies from a unicolored greenish to a unicolored dark greyish-brown. Some individuals exhibit a very distinct dark or light band with irregular margins at about the periphery, occasionally the apical part of the mantle is spotted yellowish.

Radula (Fig. 217): The B-central bears 3–4 well-defined cusps; A- and C-central are smooth or crenulate. The comb-lateral remarkably differs from other Costa Rican species in its consistently low number of only 6 cusps. Furthermore, the cusps increase considerably in size inwards. The number of denticles on the marginals increases rapidly. Radula with about 69–78 rows of teeth.

Female Reproductive System (Fig. 218): The receptaculum seminis is very small and spherical. The bursa copulatrix bears a few regular lobes; in one specimen, it is only bi-

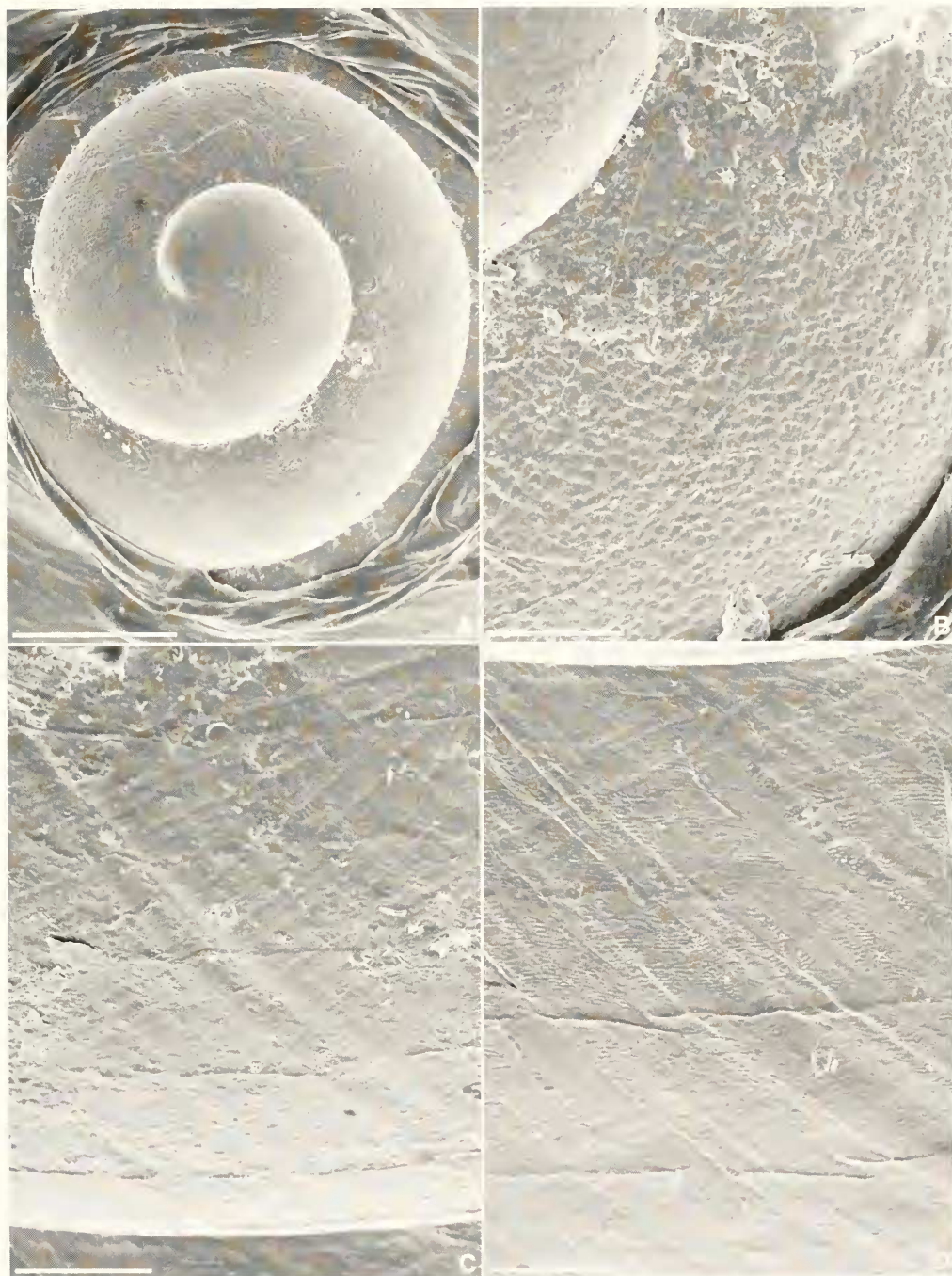


FIG. 214. Teleoconch surface structure of *Helicina escondida* n. sp. A. Embryonic shell and transition of different sections. B. Immediately after embryonic shell: transitional surface structure. C. 2nd whorl. D. 3rd whorl; scale bars 500 μ m (A), 100 μ m (B-D).

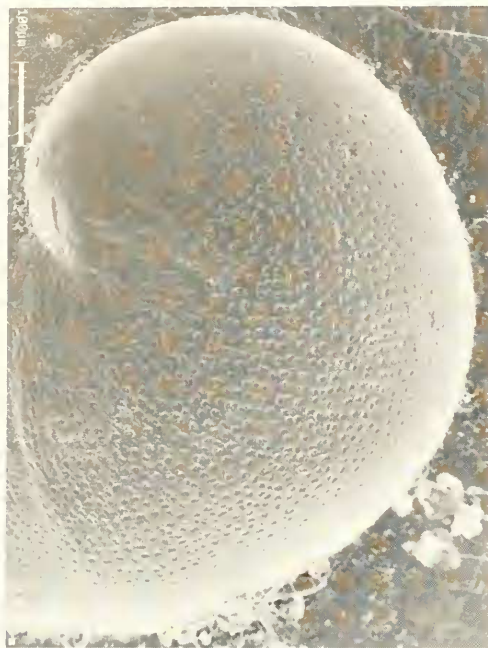


FIG. 215. Embryonic shell of *Helicina escondida* n. sp.; scale bar 100 µm.

lobed. The provaginal sac is elongated and its stout stalk joins the sac about the middle of the long side.

Morphometry and Sexual Dimorphism (Table 12, Figs. 219–223)

The sexes of all specimens from the three areas were determined. Material from INBio allowed the assignment without preparation because of the quite transparent shells.

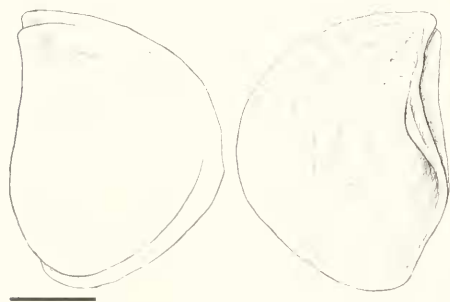


FIG. 216. Operculum of *Helicina escondida* n. sp., ZMB 103880; scale bar 1 mm.

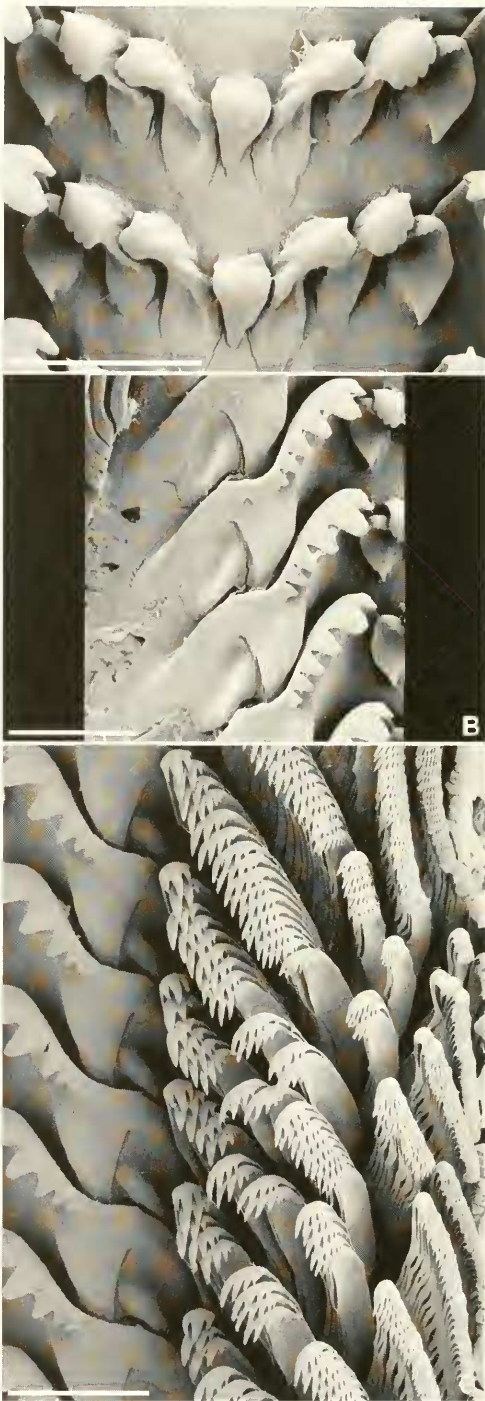


FIG. 217. Radula of *Helicina escondida* n. sp. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 µm.



FIG. 218. Female reproductive system of *Helicina escondida* n. sp., ZMB 103880; scale bar 1 mm.

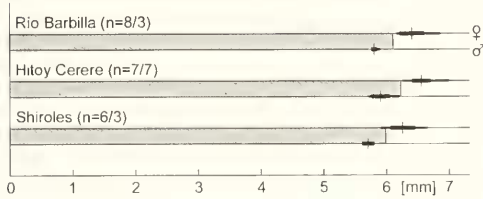


FIG. 219. Shell height of different populations of *Helicina escondida* n. sp. in Costa Rica according to Table 12; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males"; upper line: females, lower line: males; in between and shaded: average of both for comparison with populations of unknown sex.

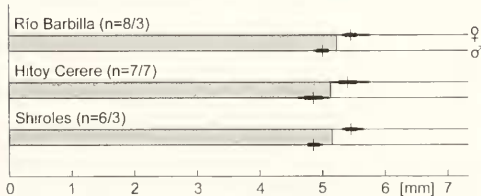


FIG. 220. Minor diameter of shell of different populations of *Helicina escondida* n. sp. in Costa Rica according to Table 12; for explanations see Fig. 219.

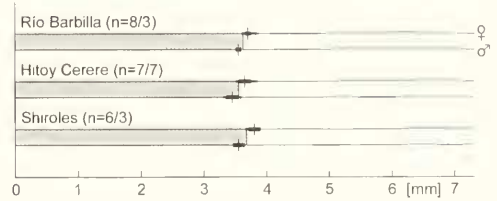


FIG. 221. Expansion of outer lip of different populations of *Helicina escondida* n. sp. in Costa Rica according to Table 12; for explanations see Fig. 219.

Morphometry: The populations show only minor deviations among each other and for the different measurements. Only the specimens from Hitoy Cerere are a little more elevated (height and height of the columellar axis).

Sexual Dimorphism: The data show a clear distinction between the measurements for sexes, with the males being much smaller (Figs. 224–226). In interpolation from the minor diameter, males have an average volume of about 74% that of the females, resembling *Helicina tenuis*.

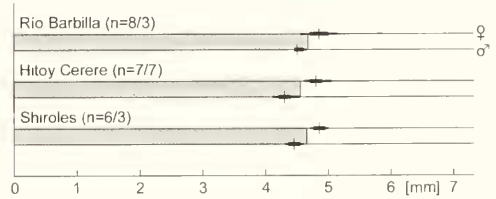


FIG. 222. Height of last whorl of different populations of *Helicina escondida* n. sp. in Costa Rica according to Table 12; for explanations see Fig. 219.

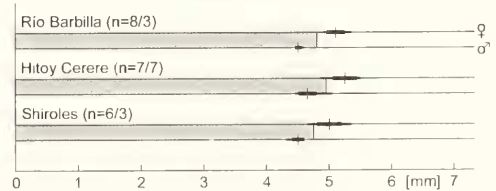


FIG. 223. Height of columellar axis of different populations of *Helicina escondida* n. sp. in Costa Rica according to Table 12; for explanations see Fig. 219.

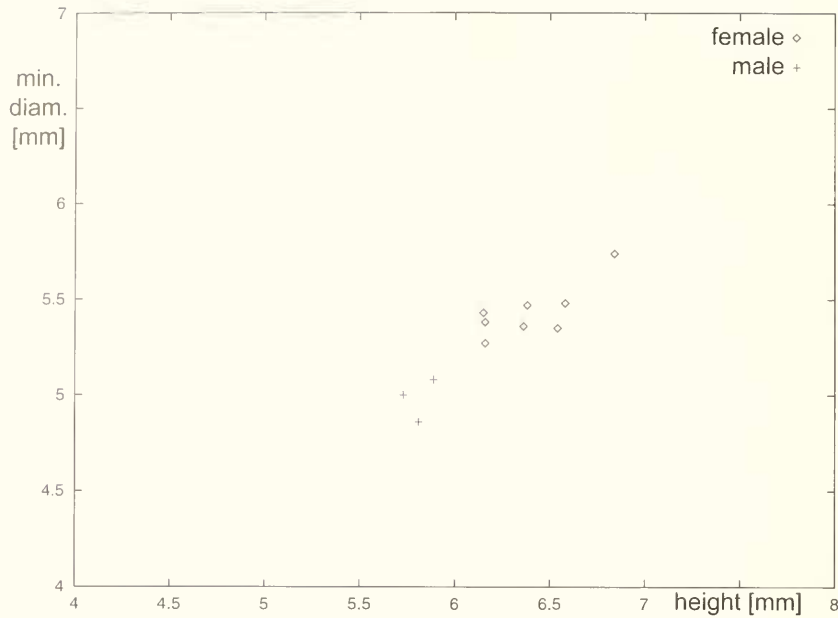


FIG. 224. Range of measurements in females and males of *Helicina escondida* n. sp. exemplary for height and minor diameter in the population from the Río Barbilla.

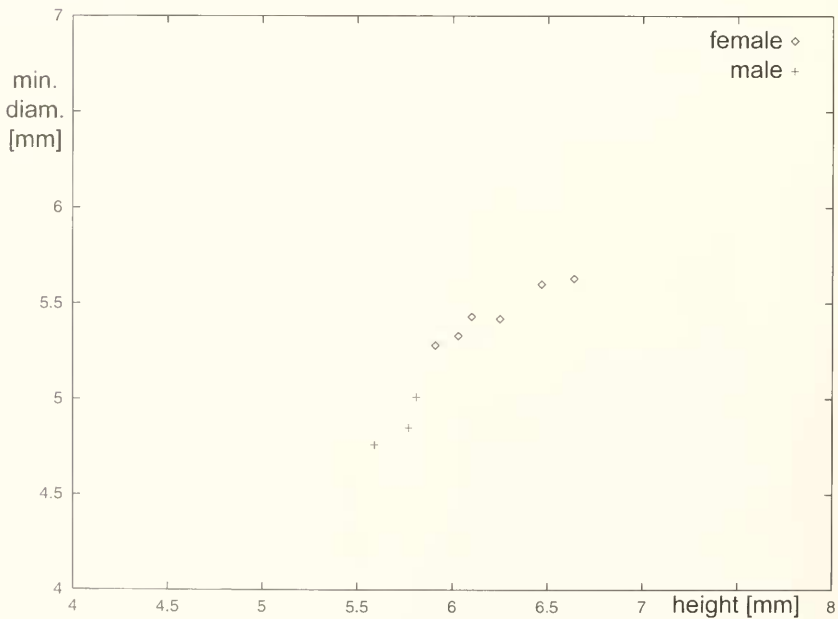


FIG. 225. Range of measurements in females and males of *Helicina escondida* n. sp. exemplary for height and minor diameter in the population from the Shiroles.

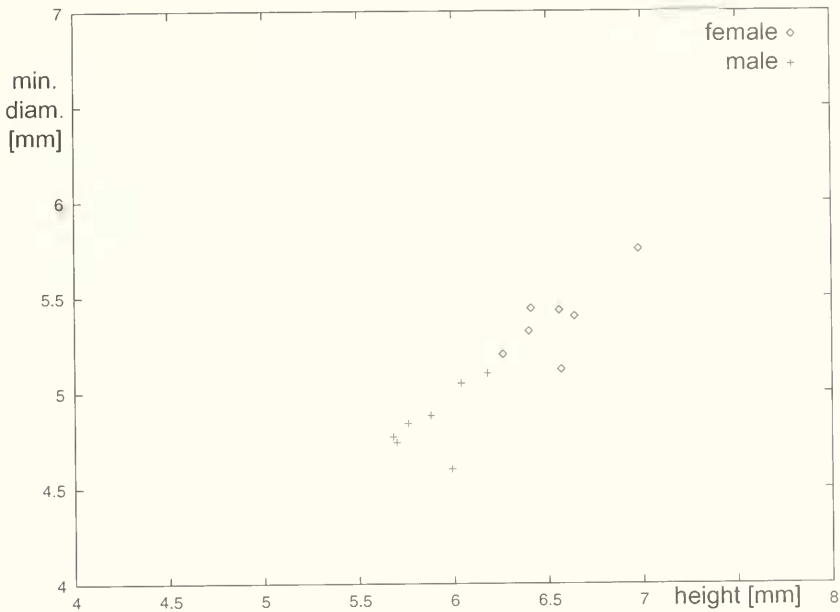


FIG. 226. Range of measurements in females and males of *Helicina escondida* n. sp. exemplary for height and minor diameter in the population from the Hitoy Cerere.

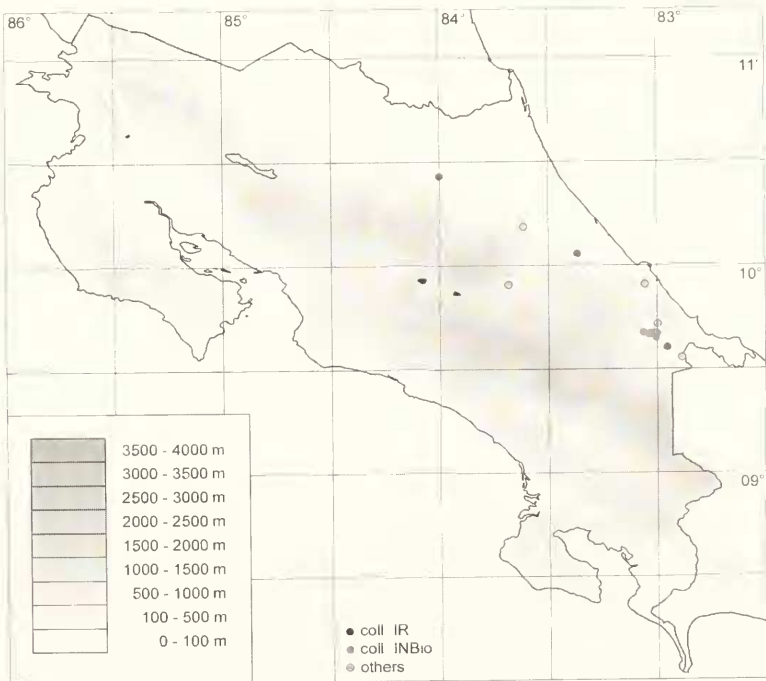


FIG. 227. Records of *Helicina escondida* n. sp. in Costa Rica.

TABLE 12. Measurements of different populations of *Helicina escondida* n. sp. given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm].

"Río Barbilla" (altitude 70 m) lot IR 1543							"Hitoy Cerere" (altitude 110–798 m) lots INBio 1466441, 1497850, 1498244, 3542523, 3091132, 3091794				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	6.40	0.19	6.15	6.84	8	6.55	0.16	6.26	6.98	7
Height	m	5.81	0.05	5.73	5.89	3	5.89	0.15	5.68	6.18	7
Maj. diam.	f	5.90	0.10	5.76	6.09	8	5.85	0.19	5.58	6.26	7
Maj. diam.	m	5.44	0.10	5.32	5.59	3	5.30	0.14	4.98	5.58	7
Min. diam.	f	5.44	0.10	5.27	5.74	8	5.38	0.14	5.12	5.75	7
Min. diam.	m	4.98	0.08	4.86	5.08	3	4.85	0.13	4.60	5.10	7
Outer lip	f	3.72	0.07	3.58	3.86	8	3.66	0.11	3.48	3.85	7
Outer lip	m	3.56	0.04	3.52	3.62	3	3.43	0.10	3.28	3.60	7
Last whorl	f	4.84	0.14	4.56	5.13	8	4.82	0.10	4.62	5.04	7
Last whorl	m	4.52	0.08	4.44	4.64	3	4.28	0.10	4.12	4.57	7
Col. axis	f	5.09	0.13	4.89	5.34	8	5.23	0.18	4.87	5.52	7
Col. axis	m	4.49	0.06	4.44	4.58	3	4.67	0.13	4.47	5.03	7

"Shiroles" (altitude 430 m) lot IR 1601						
	Sex	Mean value	Deviation	Min	Max	Number
Height	f	6.23	0.22	5.91	6.64	6
Height	m	5.72	0.09	5.59	5.81	3
Maj. diam.	f	5.95	0.08	5.86	6.18	6
Maj. diam.	m	5.38	0.09	5.24	5.51	3
Min. diam.	f	5.45	0.11	5.28	5.63	6
Min. diam.	m	4.87	0.09	4.76	5.01	3
Outer lip	f	3.79	0.08	3.67	3.93	6
Outer lip	m	3.56	0.08	3.45	3.66	3
Last whorl	f	4.84	0.11	4.69	5.01	6
Last whorl	m	4.47	0.10	4.32	4.58	3
Col. axis	f	4.99	0.18	4.67	5.37	6
Col. axis	m	4.49	0.11	4.32	4.60	3

Habitat

Helicina escondida n. sp. is an arboreal species that was found on the lower side, more seldomly, the upper side, of small-leaved undergrowth plants. It also was observed aestivating on fronds of ferns. Near the Río Barbilla, the species was only found along a small creek together with *H. chiquitica*. North of Shiroles and probably in Hitoy Cerere, it occurs sympatrically with *H. beatrix confusa* and *H. funcki*. There it was found on a ridge with forest cover.

Distribution (Fig. 227)

The species occurs on the central and southern Caribbean side of Costa Rica at some distance from the coast mainly in the slightly elevated hilly countryside. The most northern occurrence is from the northern foothills of the Cordillera Central; to the south, *Helicina escondida* n. sp. reaches the Valle de Talamanca. Between the neighboring valleys Valle de Estrella and Valle de Talamanca, the species lives up to altitudes of about 800 m.

Because undisturbed areas in this region are still relatively uninvestigated due to their inaccessible nature, it is very likely that *H. escondida* n. sp. can be found at additional localities.

Discussion

Helicina escondida n. sp. was found in at least three different colors within one population (Figs. 210–212, 336K–M): (1) unicolored yellow (represented in holotype, Fig. 336K), (2) reddish-brown, except for the umbilical area, which is whitish (represented by paratype 1, Fig. 336L), or (3) the upper half of each whorl is reddish brown, this may be very light, and the lower half yellow or only with a yellowish band, the transition of both colors exactly at the suture/ periphery, so that the yellow is only seen on last whorl (represented by paratype 2, Fig. 336M). The outer lip is constantly whitish-yellowish.

Helicina escondida n. sp. is distinguished from other small helicínids, such as *H. beatrix*, *H. talamancensis*, *H. montevertensis* n. sp., *H. fragilis*, and *H. gemma*, by the special surface structure of fine oblique lines and spiral striations. In the species mentioned, it is shiny and smooth. Furthermore, the aperture is straight and not curved backwards. Finally, the groove in the umbilical area is unique for *H. escondida* n. sp. among comparable species. (For further discussion of small, fragile, whitish-yellowish Central American Helicínidae, see the section on *H. montevertensis* n. sp.) In *H. beatrix*, the whorls are much more convex, and it has a higher spire and a distinct whitish subsutural band. *Helicina gemma* has a orange-scarlet outer lip, whereas in *H. escondida* n. sp. it is yellowish-white. At its type locality, *H. chiquitica* and *H. escondida* n. sp. occur sympatrically, but they are easily separated by their size, color, shape and shell surface texture.

Helicina ("Gemma") *chiquitica*
(Richling, 2001)

Alcacia (*Leialcacia*) *fragilis* – Wagner, 1908: 84–85: Costa Rica: Shirores, Talamanca [in part] [*non* Morelet, 1851]
Oligyra chiquitica Richling, 2001: 1–2 (text figure)

Original Description

See "Description".

Type Material

Holotype: INBio 3404977, female (leg. I. Richling, 12.3.2001)
Paratype 1: INBio 3404981, male (same data as holotype)
Paratype 2: ZMB 103386a, female (same data as holotype)
Paratype 3: ZMB 103386b, male (same data as holotype)
Dimensions (height/greatest diameter):
Holotype: 4.9/4.5 mm
Paratype 1: 4.3/4.2 mm
Paratype 2: 4.6/4.4 mm
Paratype 3: 4.3/4.1 mm

Type Locality

SE-Costa Rica, Limón Province, approximately 9 km W of Matina, a little upstream on the Río Barbilla from the crossing of the road from Siquirres to Limón, along a tributary of Río Barbilla, 10°03'29"N, 83°22'24"W, 70 m a.s.l., in the valley of a small creek in rain forest (probably secondary forest).

Examined Material

LEG. I. RICHLING

Heredia: S Puerto Viejo de Sarapiquí, *Zona Protectora La Selva*, near OTS-Station, about 10°25'53"N, 84°00'18"W, 60 m a.s.l., 05.09.1999: (IR 1662)

Limón: About 9 km W of Matina, road from Limón to Siquirres, a little stream up the *Río Barbilla*, along a tributary of Río Barbilla, in the valley of a small creek in rain forest, 10°03'29"N, 83°22'24"W, 70 m a.s.l., 12.03.2001: (IR 1539)

S Siquirres, road from Limón to Siquirres, along footpath stream up *Río Pacuarito*, in the valley of a little northern tributary, 10°05'38"N, 83°28'11"W, 110 m a.s.l., 18.03.2001: (IR 1611)

INBIO COLLECTION

Cartago: *Parque Nacional Barbilla*, Sector de la Estación de Barbilla, leg. Alexander Alvarado Mendez: 09°58'26"N, 83°27'58"W, 500 m a.s.l., 28.09.2000: 1 ad. (INBio 3100273); 09°58'24"N, 83°27'23"W, 300 m a.s.l., 30.09.2000: 1 ad. (INBio 3104239)
Zona Protectora Río Pacuare, Sector de la Estación de Barbilla, 09°58'50"N, 83°27'08"W, 500 m a.s.l., leg. Alexander Alvarado Mendez, 05.09.2000: 1 ad. (INBio 3103323)



FIG. 228. *Helicina chiquitica*, holotype, INBio 3404977, height 4.9 mm; scale bar 2 mm.

OTHER SOURCES

COSTA RICA

Limón: Shirores [Shiroles, 09°35'38"N, 82°57'20"W], Talamanca: leg. H. Pittier (#269): 1 s.ad. (MHNN, part of the lot); leg. H. Pittier (#208), 03.1895: 1 ad., 2 s.ads. (ZMB 48336, part of the lot); leg. Pittier: 1 ad. (ZMB 103250)

Etymology

The species is named for its small size. "Chiquitica" is a diminutive of "chiquita" (Spanish) = "small". In Latin America it correctly would be "chiquitita", but in Costa Rica the diminutive syllable "-tito/a" sometimes is changed to "-tico/a"; the Costa Rican people call themselves also Ticos.

Description

Shell (Figs. 228, 336N): conical-globose, thin, small, shiny. Color: unicolored, reddish-

brown, more or less transparent, towards aperture color more intensive. Periostracum very thin, shiny and smooth, except for very fine growth lines. Embryonic shell of about 1 whorl; subsequent $3\frac{3}{8}$ to 4 (holotype: $3\frac{3}{4}$) whorls slightly convex, equally extending in size; last whorl rounded at periphery. Suture slightly impressed. Aperture oblique and in its middle part slightly curved backwards. Outer lip dark red, thickened, very narrowly reflexed. Basal callus thin, in umbilical area surface scaly-granulated.

Internal Shell Structures (Fig. 229):

Teleoconch Surface Structure (Fig. 230): The transitional pattern is well developed (about $\frac{1}{2}$ of a whorl), the subsequent zone with oblique diverging grooves is short. The rest of the teleoconch is smooth, except for fine growth lines.

Embryonic Shell (Fig. 231): The structure does not exhibit peculiarities and closely resembles that of *Helicina gemma*. Compared with the shell size of the latter, the diameter of the embryonic shell of *H. chiquitica* is only slightly smaller. The embryonic shell of the clearly larger *H. escondida* n. sp. is on average even smaller (728 μ m) than that of *H. chiquitica*. This shows that embryonic shell size does not always depend on the shell size (see general discussion below). Diameter: 749 μ m (\pm 28) (660–800) (n = 25) (IR 1539).

Operculum (Fig. 232): Very slightly calcified, calcareous plate not reaching the margin.

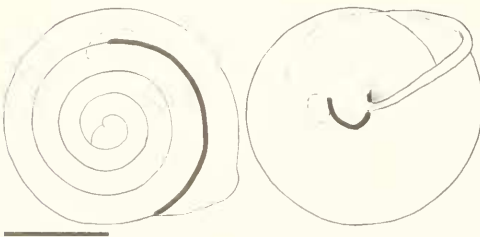
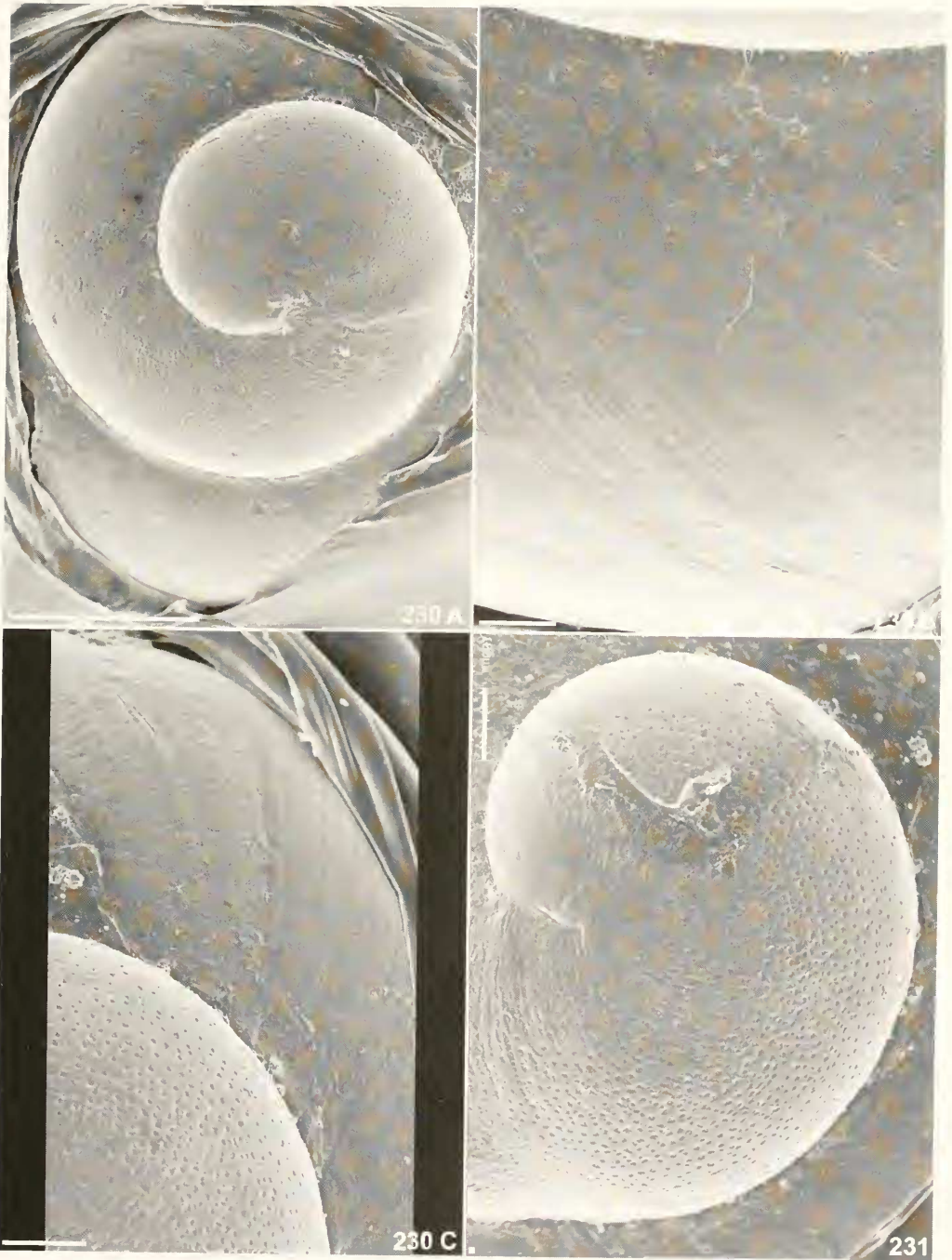


FIG. 229. Axial cleft and muscle attachments of *Helicina chiquitica*, INBio 3404977; scale bar 2 mm.



FIGS. 230, 231. Shell structure of *Helicina chiquitica*. FIG. 230 Teleoconch surface structure. A. Structure of apical part. B. 2nd whorl. C. 1st whorl: occasional sharp transition from oblique diverging grooves to smooth surface; scale bars 500 µm (A), 100 µm (B–C). FIG. 231. Embryonic shell; scale bar 100 µm.

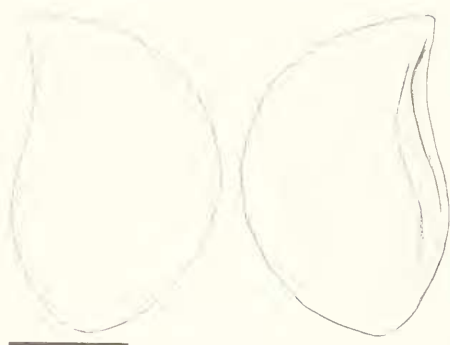


FIG. 232. Operculum of *Helicina chiquitica*, holotype, INBio 3404977; scale bar 1 mm.

Color horny-amber, slightly transparent. Columellar side S-shaped, upper end acute, lower edge rounded. On inner side, a little ridge parallel to columellar margin. Outer surface granulated.

Animal (Figs. 339C, D): The foot-head region shows a similar color to other species in being greyish-black on the dorsal half including the tentacles. The mantle pigmentation is black throughout or mottled with small pale dots mainly in the apical part. The yellow-shelled form is also much paler in the body color.

Radula (Fig. 233): All centrals lack well-defined cusps and the faces are less pronounced. Comb-lateral with 10–12 pointed cusps, a high number among the Costa Rican species. Cusps on marginals rapidly increasing in number. Radula with about 65–72 rows of teeth.

Female Reproductive System (Fig. 234): The ascending limb of the V-organ is very prominent and stout, the receptaculum seminis is rather small and oblong. The bursa copulatrix is formed by an irregular ovoid sac, which appears to be internally subdivided. The provaginal sac is simple and connected by a short duct. The pallial oviduct is relatively short.

Morphometry and Sexual Dimorphism (Table 13, Figs. 235–239)

Helicina chiquitica is the smallest arboreal species investigated in this study. The few

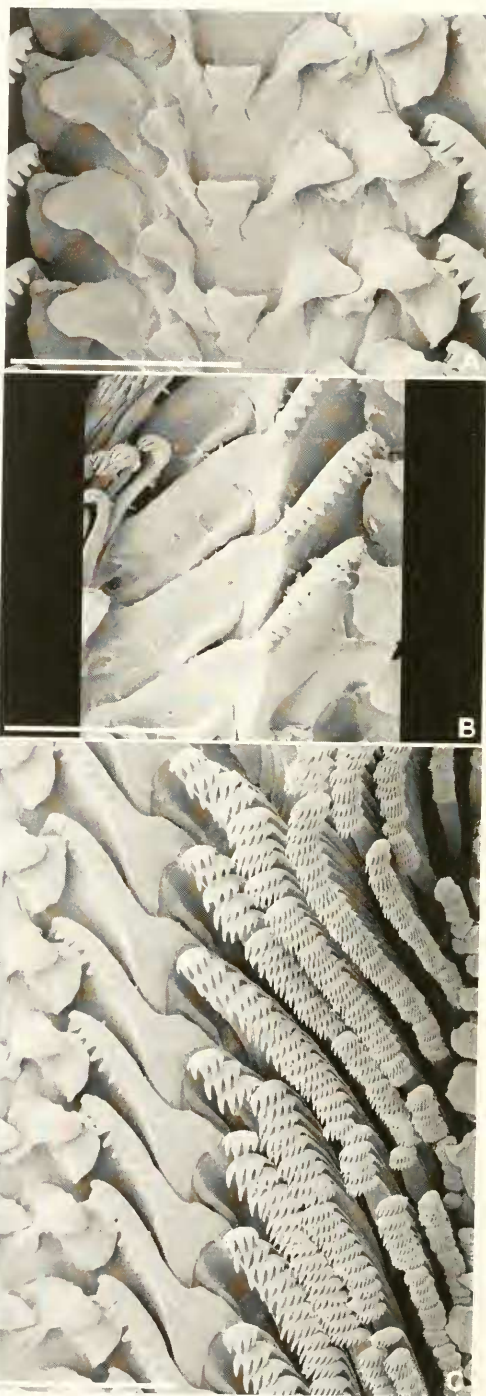


FIG. 233. Radula of *Helicina chiquitica*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 μ m.



FIG. 234. Female reproductive system of *Helicina chiquitica*, IR 1539; scale bar 1 mm.

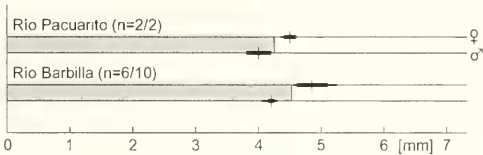


FIG. 235. Shell height of the two populations of *Helicina chiquitica* in Costa Rica according to Table 13; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males"; upper line: females, lower line: males; in between and shaded: average of both for comparison with populations of unknown sex.

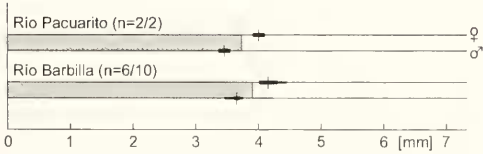


FIG. 236. Minor diameter of shell of the two populations of *Helicina chiquitica* in Costa Rica according to Table 13; for explanations see Fig. 235.

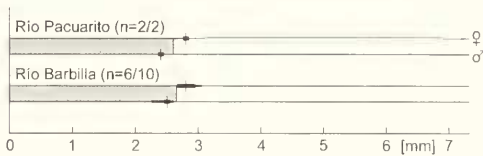


FIG. 237. Expansion of outer lip of the two populations of *Helicina chiquitica* in Costa Rica according to Table 13; for explanations see Fig. 235.

specimens of *H. chiquitica* from two different localities suggest a smaller shell size for the site "Rio Pacuarito", but the sample size is small.

On the other hand, sexual dimorphism is undoubtedly indicated. The clear distinction between the sexes is also illustrated at "Rio Barbilla" (Fig. 240). In the interpolation from the minor diameter, males have an average volume of about 65% of that of females.

Habitat

The species has mainly been found on the lower side of leaves of Araceae, occasionally also on the leaves of bushy plants of the undergrowth. At Río Barbilla and Río Pacuarito,

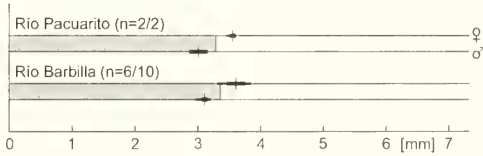


FIG. 238. Height of last whorl of the two populations of *Helicina chiquitica* in Costa Rica according to Table 13; for explanations see Fig. 235.

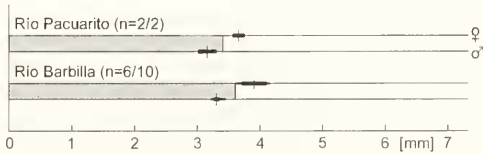


FIG. 239. Height of columellar axis of the two populations of *Helicina chiquitica* in Costa Rica according to Table 13; for explanations see Fig. 235.

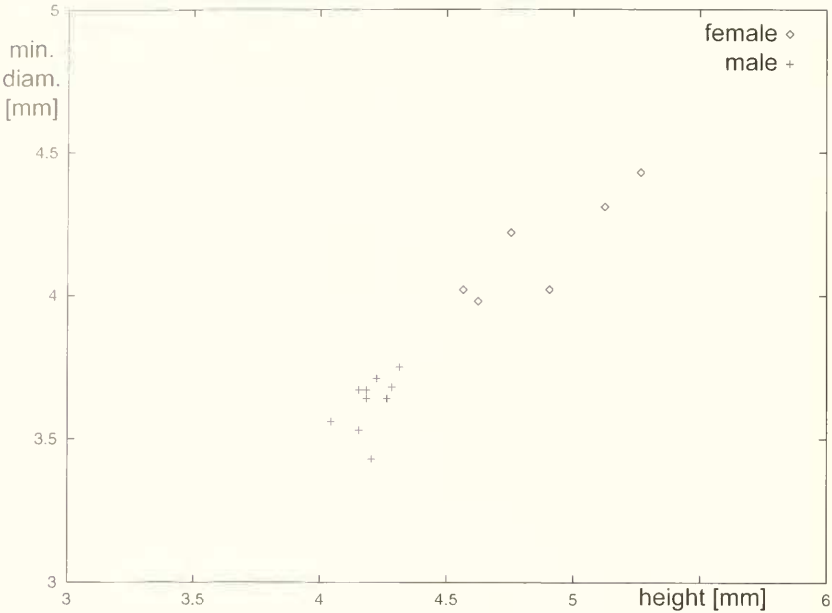


FIG. 240. Range of measurements in females and males of *Helicina chiquitica* exemplary for height and minor diameter in the population from the Río Barbilla.

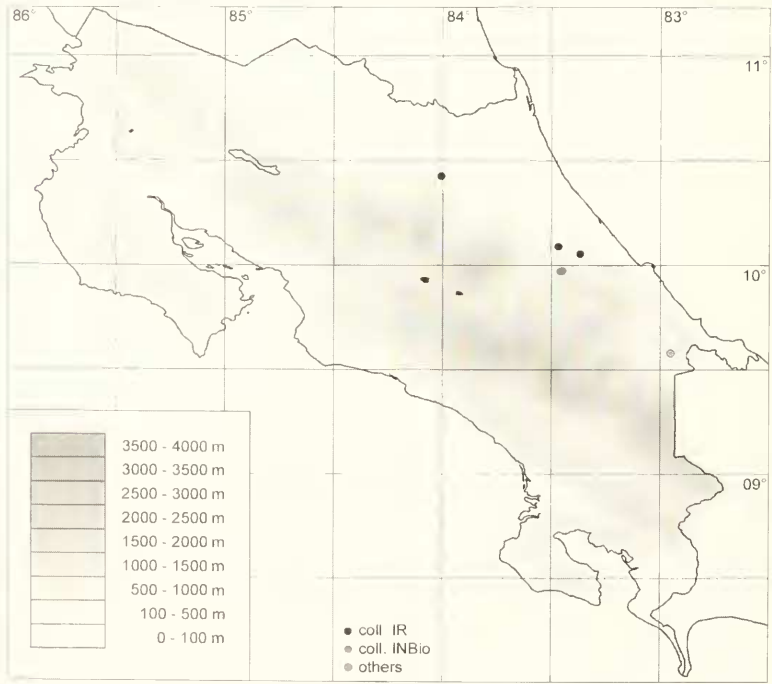


FIG. 241. Records of *Helicina chiquitica* in Costa Rica.

TABLE 13. Measurements of the two populations of *Helicina chiquitica* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens (min./max. diam. = minor/major diameter, col. axis = columellar axis); linear measurements [mm], weight [g], volume [ml].

"Río Barbilla" (altitude 70 m) lot IR 1539							"Río Pacuarito" (altitude 110 m) lot IR 1611				
	Sex	Mean value	Deviation	Min	Max	Number	Mean value	Deviation	Min	Max	Number
Height	f	4.87	0.23	4.56	5.26	6	4.49	0.12	4.37	4.60	2
Height	m	4.20	0.06	4.04	4.31	10	3.99	0.21	3.78	4.20	2
Maj. diam.	f	4.48	0.13	4.33	4.68	6	4.33	0.06	4.26	4.39	2
Maj. diam.	m	3.97	0.10	3.73	4.16	10	3.72	0.13	3.59	3.84	2
Min. diam.	f	4.16	0.16	3.98	4.43	6	4.01	0.09	3.92	4.09	2
Min. diam.	m	3.63	0.07	3.43	3.75	10	3.44	0.09	3.35	3.53	2
Outer lip	f	2.82	0.13	2.64	3.04	6	2.78	0.04	2.74	2.82	2
Outer lip	m	2.49	0.07	2.27	2.61	10	2.42	0.04	2.38	2.45	2
Last whorl	f	3.61	0.14	3.38	3.84	6	3.54	0.07	3.47	3.61	2
Last whorl	m	3.10	0.05	2.94	3.20	10	3.01	0.13	2.88	3.13	2
Col. axis	f	3.88	0.18	3.60	4.17	6	3.64	0.10	3.54	3.74	2
Col. axis	m	3.32	0.07	3.18	3.44	10	3.15	0.17	2.98	3.31	2

the occurrence seems to be confined to the vegetation along small, partly steep creeks. At the former locality, *Helicina chiquitica* lives sympatrically with *H. escondida* n. sp.

Distribution (Fig. 241)

Except for the single record northeast of the Central Cordillera, the few records are in the most northern part of the Caribbean foothills of the Cordillera de Talamanca. *Helicina chiquitica* has only been found some distance from the coast in the hilly countryside from elevations of 70 m to 500 m. The undisturbed areas in this region have scarcely been investigated, because they are difficult to reach. The northern record renders it also very likely that *H. chiquitica* will be found at additional localities.

Furthermore, the small size and the rapid decay of shells in a humid tropical climate provide grounds for assuming that the species has a wider distribution than actually been documented. A study by Barrientos (2000) for *Ovachlamys fulgens* (Gude, 1900) suggests that shells decay in less than five months in the climate of San José with 5–6 dry months per year as opposed to the Caribbean slope, where, lacking dry months, it would take place even faster.

Discussion

In some specimens, the apex is reddish-brown, but the subsequent whorls are yellow. In this case the outer lip is yellow too.

In its shape and shell sculpture, *Helicina chiquitica* is comparable to *H. gemma*, *H. monteverdensis* n. sp., and *H. fragilis*, but *H. chiquitica* is much smaller and has a different color. None of the two species mentioned shows such a dark color in combination with a dark outer lip. The size of the new species is exceptionally small for the known Central American heliciniids of this shape. *Helicina strebeli* L. Pfeiffer, 1861, is another small heliciniid from Mexico, generally treated as a small subspecies or variety of *Helicina flavida* (see von Martens, 1890; Fischer & Crosse, 1893; Baker, 1928), which clearly differs by its spiral striation. *Helicina mohriana* L. Pfeiffer, 1861, described from Orizaba, Mexico, is discussed as a dubious species or perhaps juvenile stage by Martens (1891) and Fischer & Crosse (1893) or as a synonym of *Helicina fragilis merdigera* by Baker (1922a) respectively. According to the original description, however, it is a little broader than it is high, whereas in *H. chiquitica* all specimens show the reverse relation. Furthermore *H. mohriana* seems to have more whorls (5.5) than the new

species, for which 5 (4 plus about 1 of embryonic shell) whorls are exceptional.

The record of Wagner (1908) for Shiroles in Costa Rica had been based on the material in the ZMB, since the specimens carried determinations written by Wagner. Reexamination of the material revealed specimens of *H. chiquitica*, but the lot (and a similar lot of Pittier stored in the MHNN) consists of two different species, where, unfortunately, all deviating specimens are immature. They exhibit very strong spiral cords, but do not seem to represent *H. escondida* n. sp. which has recently been found at Shiroles, whereas *H. chiquitica* has not as yet been discovered there.

Pyrgodomus microdinus
(Morelet, 1851)

Helicina microdina Morelet, 1851: 18 (not figured)

Helicina microdina – L. Pfeiffer, 1852a: 354

Helicina microdina – L. Pfeiffer, 1852b: 256

Helicina chryseis Tristram, 1862: 5: Guatemala: mountain forests of Vera Paz (Salvin) (not figured)

Helicina microdina – Bland, 1866: 8

Helicina chryseis – Bland, 1866: 10

Helicina chryseis – von Martens, 1890: 39, pl. I, fig. 14

Helicina microdina – von Martens, 1891: 42 (dubious species)

Helicina (Pyrgodomus) chryseis – Fischer & Crosse, 1893: 440, pl. LVII, fig. 6

Helicina (Idesa) microdina – Fischer & Crosse, 1893: 438–439, pl. LVI, fig. 9

Helicina chryseis – von Martens, 1900: 606

Eutrochatella (Artecallosa [sic]) microdina – Wagner, 1908: 138–139, pl. 20, figs. 17–20

Eutrochatella microdina chryseis – Pilsbry, 1920b: 197: Guatemala: Chama

Eutrochatella microdina [sic] var. *chryseis* – Hinkley, 1920: 52: Guatemala: Alta Verapaz: Chama between Río Tsalbha and Río Negro Chama: also in river drift

Eutrochatella (Pyrgodomus) microdina microdina – Baker, 1922a: 61

Eutrochatella (Pyrgodomus) microdina chryseis – Baker, 1922a: 61 (may be a sex-form)

Pyrgodomus microdinus chryseis – Baker, 1928: 45–46

Pyrgodomus microdinus microdinus – Baker, 1928: 45–46

Pyrgodomus microdina – Goodrich & van der Schalie, 1937: 13, 33: Guatemala: Petén: region of headwater of Río San Pedro de Mártir, lower Río de la Pasión; Alta Verapaz: upper part of Río de la Pasión

Pyrgodomus ? spec. – Monge-Nájera, 1997: 113: Costa Rica

Synonymy

Helicina chryseis Tristram, 1862

Original Description

"T. parvula, conica, transversim minute striata, spiraliter lirata, flava, sursum saturatior. Anfr. 6 convexi, ultimo angulato; columella arcuata, superne callosa, subdilata. Apertura obliqua, ovalis, margine simplici, recto.



FIG. 242. *Helicina microdina*, lectotype, BMNH 1893.2.3.1986, height 3.8 mm; scale bar 1 mm.

Altit. 4. – Diam. 4.

H. vulgaris prov. Vera-Paz.

Primo aspectu *H. rupestris* Pfr. congruit, quamvis in universum ab ea dissimilis."

Type Material

BMNH 1893.2.3.1986–90: Morelet coll., purchased from H. Fulton

The Morelet collection was bought by H. Fulton and later purchased by the BMNH. Fischer & Crosse (1893) studied the original material in Morelet collection and figured one shell which can be identified by the mark of a "x". This shell is **here selected as lectotype** of *Helicina microdina* (BMNH 1893.2.3.1986) (Fig. 242), because it is uncertain whether Fischer & Crosse's comment in the figure caption (pl. LVI, figs. 9, 9a, 9b, 9c: "Type de l'*H. microdina*") can be regarded as a type selection.

Dimensions (height/greatest diameter/minor diameter):

Lectotype BMNH 1893.2.3.1986: 3.8/3.9/3.5 mm

Type Locality

"Vera-Paz" [Guatemala, Alta Verapaz Department].

Examined Material

LEG. I. RICHLING

Puntarenas: *N Neily*, road from Ciudad Neily to San Vito, open area with a few trees, 08°40'23"N, 82°56'44"W, 180 m a.s.l., N Neily, 23.03.1997: (IR 209)

Fila de Cal, road from Ciudad Neily to San Vito: S Campo Dos, burned area and ground with secondary growth and limestone rocks, 08°41'00"N, 82°56'29"W, 630 m a.s.l.: 23.03.1997: (IR 192); 07.03.1998: (IR 502); 09.02.2000: (IR 1147); Campo Dos, on Finca, secondary growth and limestone rocks, 08°41'16"N, 82°56'38"W, 700 m a.s.l.: 07.03.2001: (IR 1517)

INBio COLLECTION

Puntarenas: *Fila Cal*, 24 km de San Vito hacia Ciudad Neily, 08°41'36"N, 82°56'36"W, 780 m a.s.l., 14.01.1995: leg. Francisco Alvarado: 1 spec. (INBio 1480755); 1 spec. (INBio 1495177); leg. Annia Picado: 2 spec. (INBio 1481148); leg. Mario Chinchilla: 1 spec. (INBio 1481257); leg. Socorro Avila: 3 spec. (INBio 1481361); leg. Ronald Villalobos: 6 spec. (INBio 1481512); leg. Marcos Moraga: 4 spec. (INBio 1481563); leg. Oscar Esquivel: 5 spec. (INBio 1485112); leg. Marcos Madrigal: 2 spec. (INBio 1495685); leg. Enia Navarro: 1 spec. (INBio 1495695); 29.08.1995: leg. Marianella Segura: 11 spec. (INBio 3307036); 24.5 Km S en la carretera de San Vito hacia Ciudad Neily, 08°40'55"N, 82°56'23"W, 600 m a.s.l.: leg. Zaidett Barrientos, 21.11.1995: 1 spec. (INBio 1485119)

Description

Shell (Figs. 243, 336R): Conical, high-elevated, triangular in general shape, solid, small sized, dull. Color: bright yellow and on

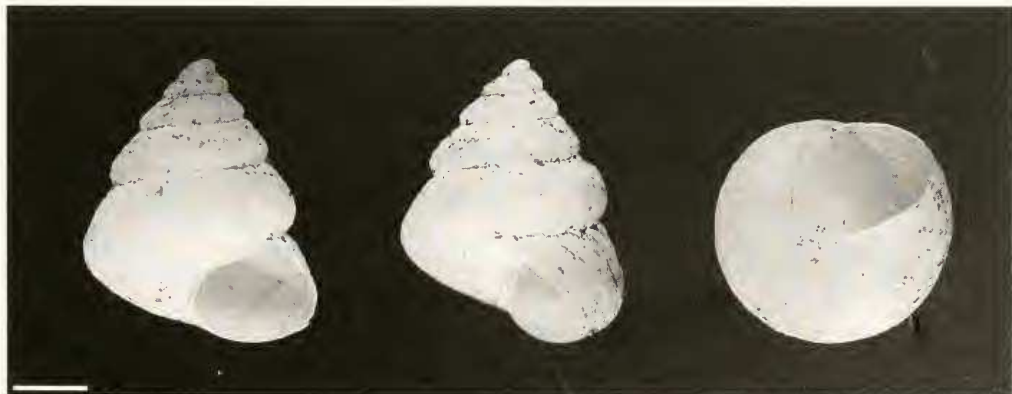
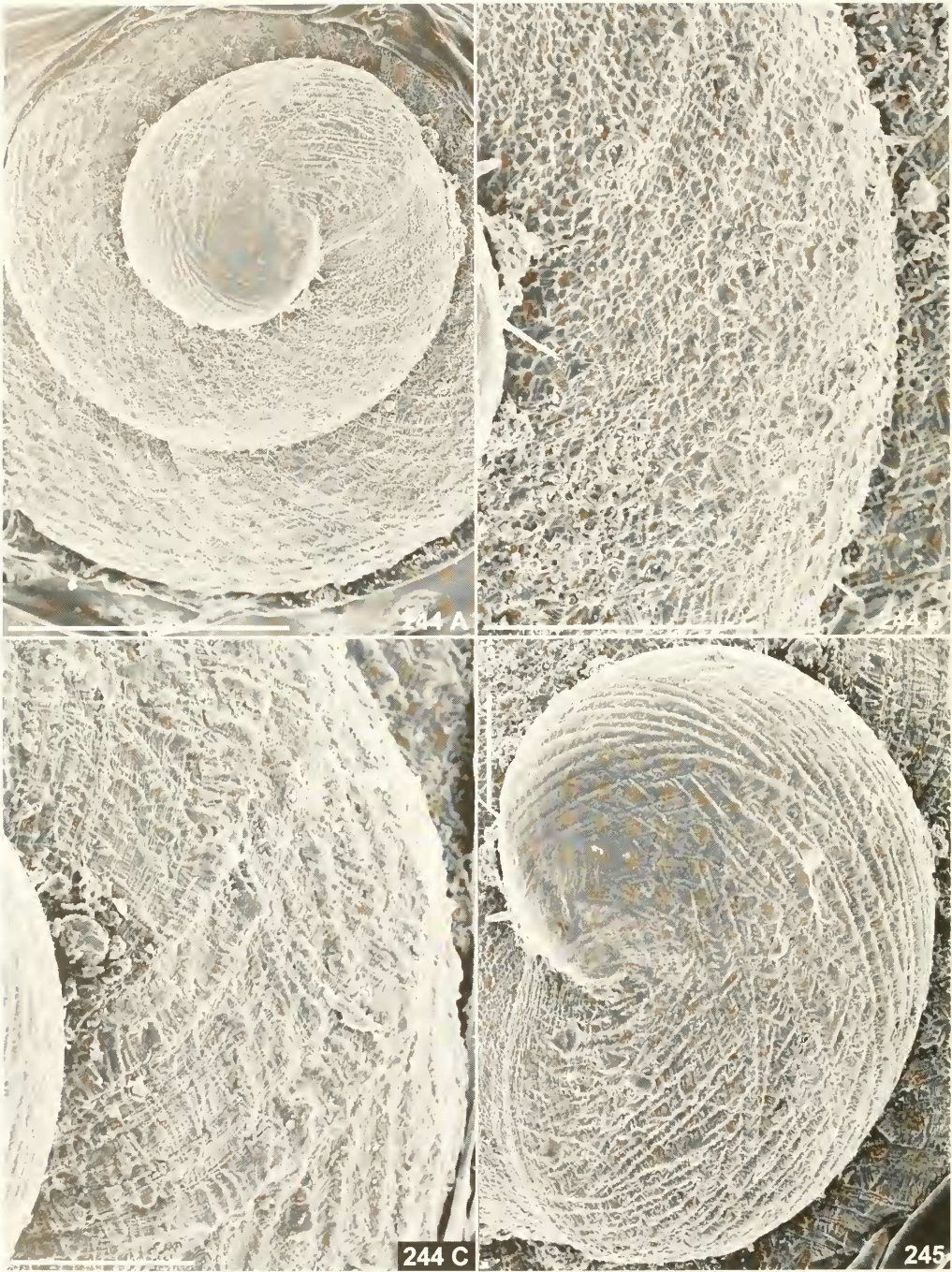


FIG. 243. *Pyrgodomus microdinus*, Fila de Cal, IR 1517, height 3.8 mm; scale bar 1 mm.



FIGS. 244, 245. Shell structure of *Pyrgodomus microdinus*. FIG. 244. Teleoconch surface structure. A. apical part. B. 1st whorl, transitional structure. C. 1st whorl, structure of postembryonic shell; scale bar 500 µm (A); 100 µm (B–C). FIG. 245. Embryonic shell; scale bar 100 µm.

upper side darker colored. Whorls sculptured with spiral ridges, very rough and irregular growth lines and oblique striations. Embryonic shell with about 1 whorl; about $4\frac{1}{2}$ subsequent whorls straight; last whorl angulated on periphery. Whorls equally increasing in size and rapidly descending, always inserting a little below periphery, forming a high, pointed, stepped spire. Suture deeply impressed. Aperture oblique and rather straight. Outer lip of same color as preceding whorls, neither remarkable thickened nor shortly expanded or reflected. Columella short and arched. Basal callus weakly developed.

Internal Shell Structures: Sufficient adult material was not available, especially because the thickness of the whorls would have required cracking the shell in order to examine the internal structures.

Teleoconch Surface Structure (Fig. 244): In *Pyrgodomus microdinus*, a structured transitional zone similar to that of the Costa Rican species of *Helicina* is developed for a certain distance at the very beginning of the teleoconch. This zone exhibits a very rough irregular surface of numerous small denticles. The following whorls bear spiral ridges crossed by irregular growth lines that are wrinkled throughout.

Embryonic Shell (Fig. 245): *Pyrgodomus microdinus* displays a greatly different embryonic shell surface structure. Coarse oblique diverging grooves cover the embryonic shell resulting in a very rough surface. Diameter: $530\text{ }\mu\text{m}$ (± 13) (510–550) ($n = 4$) (IR 192, IR 1517).

Operculum: Calcified portion strongly developed, horny plate very thin and slightly larger, columellar side of calcareous plate slightly convex and thickened. Color whitish and only very slightly transparent. Nucleus nearly in central position, and growth lines almost concentric.

Animal (Fig. 339E): The whole snout and the underside of the foot is whitish-yellowish, the latter darkens gradually to grey towards the upper side. The tentacles are of the same grey, which becomes diffuse at the bases, so that between the tentacles and behind the eyes the head region is tinged with the

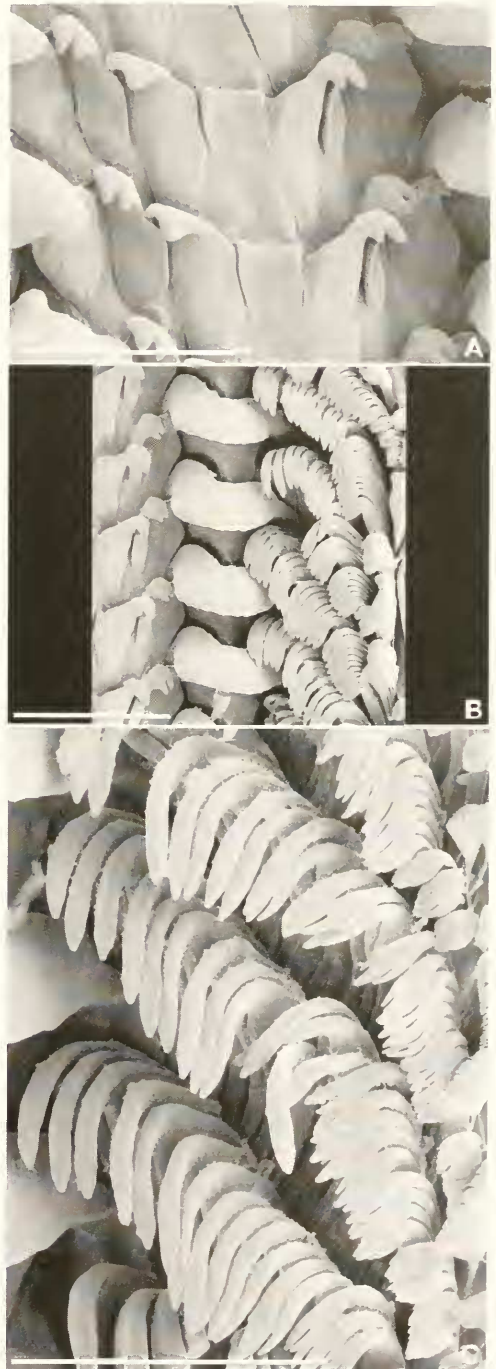


FIG. 246. Radula of *Pyrgodomus microdinus*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar $50\text{ }\mu\text{m}$.

lighter color of the snout. The mantle bears dark patches, which shine through the shells in live specimens and result in a greenish-grey appearance of the animals.

Radula (Fig. 246): Since sufficient Costa Rican material was not available, a specimen from Honduras (Colón Depto., limestone hill, 3 km WSW La Brea, 100 m a.s.l., leg. F.G. Thompson et al. (FGT-5389), 10.03.1994 (UF 221175) was studied.

R-central quadrangular; A- and B-central each bearing 2 sideways projecting cusps; C-central with 3 denticles. Comb-lateral strong developed and T-shaped with minor crenulations at the cutting edge. Inner marginals unicuspid, outwards slowly increasing number of slender, rather terminal cusps. Radula with about 130 rows of teeth. Baker (1928) studied the radula of the smaller Mexican *Pyrgodomus microdinus abditus* Baker, 1928, and described bicuspid inner marginals, which necessitated a change in the original definition of the subfamily Vianinae with unicuspid inner marginals. Furthermore, the centrals bear each one cusp more, and the denticles on the cutting edge of the T-lateral are more pronounced. It remains questionable whether these deviations are typical for the Mexican subspecies alone, or whether the

single specimen investigated in this study is representative at all or if they are subject to individual variation. The increased number of cusps in the smaller Mexican subspecies could also be caused by the phenomenon that smaller specimens/species of Helicinidae independently from their phylogenetic position show a tendency to develop more cusps (see general Discussion).

Female Reproductive System: In Costa Rica, no adult live specimens could be found, only some juveniles, therefore their anatomy could not be investigated.

Baker (1928) (reproduced here in Fig. 247) gave a description of the female reproductive system of *Pyrgodomus microdinus abditus*: The apical part of the V-organ is slightly elongated (apical swelling) and the small spherical receptaculum seminis is situated near the middle of the dorsal side of the descending limb (not visible in his figure). The bursa copulatrix is formed by a long ellipsoid sac; the bigger, rounded triangular provaginal sac exhibits coarse lobes on its distal margin. Provaginal duct and vagina are not explicitly mentioned or shown (Fig. 247, arrow), but they are believed to open into the hypobranchial duct, which orifice lies at about $\frac{1}{5}$ to $\frac{1}{6}$ of the length of the pallial oviduct. In the light of the newly discovered absence of provaginal opening in the Costa Rican species of *Helicina*, this question remains open for *P. microdinus abditus* pending further investigation. The close relationship to *Eutrochatella*, which is indicated by a similar embryonic shell structure, suggests the absence of a provaginal opening, because it is undeveloped in this genus (see under *Eutrochatella* below).

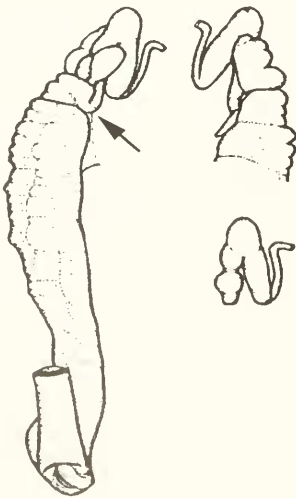


FIG. 247. Female reproductive system of *Pyrgodomus microdinus abditus*, reproduced from Baker (1928: pl. IV, figs. 21–23).

Morphometry and Sexual Dimorphism

Pyrgodomus microdinus was not found in sufficient numbers. In addition, most specimens were not fully grown, making a morphometric investigation impossible.

Habitat

Like related species (e.g., species of the genus *Eutrochatella*), *Pyrgodomus microdinus* lives on limestone rock faces and this obvious dependence characterizes the species as calciphile. Goodrich & van der Schalie (1937)

reported the species from Guatemala as being restricted to limestone outcrops. Under dry weather conditions, it was found aestivating on the underside of larger pieces of rocks or on shaded vertical sides and crevices of rocks.

Live specimens of *P. microdinus* are perfectly adapted to the background, because they possess a camouflage. Small particles of the surroundings are glued on the rough shell surface. This behavior was also observed in Guatemalan specimens by Goodrich & van der Schalie (1937). Only dead specimens show the bright yellow color.

Distribution

The Costa Rican occurrence seems to be limited to the area of the Fila de Cal north of Ciudad Neily (Fig. 248). In view of its ecological requirements, this distribution clearly reflects geological conditions. In Costa Rica, calcareous outcrops are only found in a very few places, such as the Fila de Cal.

The type locality of *P. microdinus* is Alta Verapaz, Guatemala. It has also been recorded from Péten in Guatemala and southern Veracruz, Mexico (as the subspecies *P. microdinus abditus*). For Belize, the different species, *P. simpsoni* (Ancey, 1886), is mentioned by Haas & Solem (1960). The Costa Rican populations seem to represent the most southerly occurrence of *P. microdinus*.

Discussion

Fischer & Crosse (1893) figured the species for the first time on the basis of the original Morelet material. They remarked on the similarity to *Pyrgodomus chryseis*, with the difference that the latter species is more elevated. However, they placed these species in different sections (*Idesa* and *Pyrgodomus*). Wagner (1908) proposed the synonymy of these taxa. Baker (1928) morphometrically compared *P. microdinus*, *P. chryseis* and populations from Veracruz, Mexico. As the result, he attributed the taxa to subspecific rank and raised a new

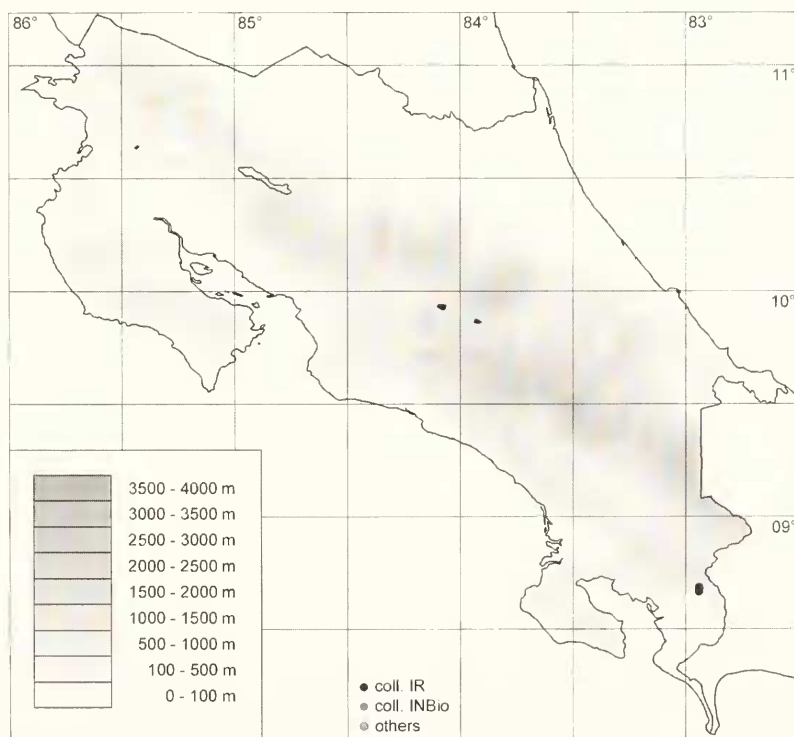


FIG. 248. Records of *Pyrgodomus microdinus* in Costa Rica.

subspecies for Mexican specimens, *P. microdinus abditus* having a smaller size, fewer whorls, and a more depressed shape. He noted that subspecific recognition of *P. microdinus chryseis* was uncertain and required study of a larger series. Ancey (1886) described a quite similar species from Isla de Utila off Honduras, *P. simpsoni*, which Baker (1928) treated as specifically distinct.

The very few adult Costa Rican specimens are remarkably elevated. Therefore, they more closely resemble *P. chryseis*. Against this historic background and because *P. chryseis* and *P. microdinus* both typically originate from the same area in Guatemala, it is more appropriate to regard them as synonymous until better knowledge of the distribution becomes available, thereby treating the Costa Rican specimens as *P. microdinus*. The geographical distance to the northern populations is uncertain due to the lack of extensive investigations of the Nicaraguan malacofauna.

***Alcadia (Microalcadia)*
Richling, n. subgen.**

Type Species

Helicina hojarasca Richling, 2001

Diagnosis

Shell very small, fragile, with fine spiral stria-tions and rows of periostracal hairs; outer lip of adults not differentiated from the whorl. Calcareous layer of the operculum very thin. Embryonic shell with irregular axial threads and fine oblique grooves crossing each other. Comb-lateral of radula with numerous cusps. Female reproductive system with provaginal opening; provaginal duct very short, thin; bursa copulatrix very prominent; ascending limb of V-organ elongated, curved; receptaculum seminis on descending limb displaced to the ventral side and directed posteriorly.

Etymology

The name refers to the small size of members of this subgenus.

Discussion

The characters of the female reproductive system, in combination with the embryonic

shell surface sculpture clearly assign the new subgenus to the genus *Alcadia* and distinguish it from *Helicina* and *Schasicheila*, which also may have been considered. Details about the characteristics of these genera as well as on other Central American supraspecific taxa, are given below.

The only subgenus which has not been included due to its South American occurrence and the absence of material for study is *Trichohelicina* Weyrauch, 1966 (type species by original designation: *Helicina (Trichohelicina) klappenbachii* Weyrauch, 1966, NE-Argentina, Misiones Province). In the light of the unexpected higher supraspecific diversity among the South American Helicinidae, such as *Angulata*, assignment to *Helicina* by Weyrauch (1966) certainly requires a critical reinvestigation, because it is only based on an impression in the basal callus. The hairy periostracum in both subgenera is regarded as a typical ecological adaptation of several ground-dwelling species and does not primarily indicate a closer relationship. In the absence of further morphological data for *Trichohelicina*, the main differences are the peculiar parietal canal in the upper edge of the aperture and the differentiated outer lip which are absent in *Microalcadia* n. subgen.

***Alcadia (Microalcadia) hojarasca*
(Richling, 2001)**

Helicina hojarasca Richling, 2001: 5–6 (text figure)

Type Material

Holotype: INBio 3404979, (leg. I. Richling, 14.8.1999)

Paratype 1: ZMB 103387 (same data as holotype)

Dimensions (height/greatest diameter):

Holotype: 2.4/2.9 mm

Paratype 1: 2.2/2.8 mm

Type Locality

NW-Costa Rica, Guanacaste Province, Cordillera de Tilarán, about 9 km N of Santa Elena, near Mirador Gerardo, 10°22'19"N, 84°48'25"W, 1,450 m a.s.l., primary cloud forest.

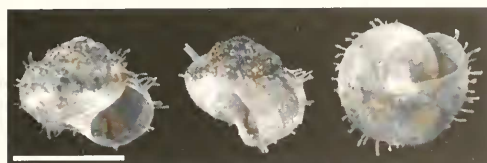


FIG. 249. *Alcadia hojarasca*, holotype, INBio 3404979, height 2.4 mm; scale bar 2.5 mm.

Examined Material

LEG. I. RICHLING

Guanacaste: About 9 km N Santa Elena, Sendero at Mirador Gerardo, 10°22'19"N, 84°48'25"W, 1,450 m a.s.l.: 14.08.1999: (IR 933)

Puntarenas: Punarenas: Zona Protectora Arenal-Monte Verde: Reserva Biológica Bosque Nuboso Monte Verde (about 10°18'08"N, 84°47'41"W, 1,500–1,650 m a.s.l.): 25.02.2001: (IR 1453)

Etymology

The species is named for its habitat "hojarasca" (Spanish) = "leaf litter", it is used as a noun in apposition.

Description

Shell (Figs. 249, 250, 336O): Very small, globose, fragile. Color yellowish-brown. Embryonic shell with about 1 whorl, without clearly marked transition to adult shell; subsequent whorls 3 to $3\frac{1}{3}$, regularly increasing in size. Surface with fine spiral cords that are axially crossed by coarse periostracal folds that form hairs at regular distances, so that the whorls bear spiral rows of hairs; 4 rows present on body whorl, on previous whorls the upper 2 rows still present. Hairs rather thick and towards the end extending in breadth, spatula shaped (Fig. 259B). Basal callus whitish and near columella surface



FIG. 250. *Alcadia hojarasca*, holotype, INBio 3404979, height 2.4 mm; scale bar 1 mm.



FIG. 251. Teleoconch surface structure of *Alcadia hojarasca*, 2nd whorl; scale bar 100 μ m.

granular. Aperture oblique, rather straight. Outer lip not differentiated from whorl, appearing like not fully grown.

Internal Shell Structures: Could not be investigated.

Teleoconch Surface Structure (Fig. 251): The coarse, irregular axial threads on the inner curvature of the embryonic shell continue for about a half whorl on the teleoconch before transforming to the typical, numerous spiral cords.

Embryonic Shell (Fig. 252): The inner curvature is sculptured with coarse, irregular axial threads; the marginal part shows numerous fine, oblique grooves crossing each other. A pitted structure does not occur. Diameter: 566 μ m ($n = 1$).

Operculum (Fig. 253): Thin, only slightly calcified, calcareous plate only covering the central area. Columellar margin irregularly S-shaped, upper edge acute, but rounded, at lower edge columellar margin continuously changing into outer margin. Nearly transparent, whitish-amber colored. Inner side with a little ridge parallel to the columellar margin.

Animal (Fig. 339F): The color is not very unusual, mantle and upper side of the foot and head region are greyish, towards the underside it becomes paler.

Radula (Fig. 254): Only two specimens were studied and the mounting procedure was

difficult due to the small size and preservation conditions. B-central with 6 small cusps; C-central rather crenulate; R- and A-central not seen. Comb-lateral with 11–12 pointed denticles, accessory plate relatively larger than in other species, about the size of the comb-lateral. Cusps on marginals rapidly increasing in number. Number of rows not counted.

Female Reproductive System (Fig. 255): The ascending limb of the V-organ is elongated and curved; the receptaculum seminis is translocated to the ventral side of the descending limb and directed upwards posteriorly. Bursa copulatrix and provaginal sac exhibit a simple structure, with the former being much larger and approximately reaching the top of the V-organ. Their connections to the reception chamber are very close to each other; at the same point enters a very slender, relatively short provaginal duct.

Morphometry and Sexual Dimorphism

On one hand, the material available is scanty, while, on the other, the peculiar lack of the development of a differentiated outer lip of



FIG. 252. Embryonic shell of *Alcadia hojarasca*; scale bar 100 μ m.

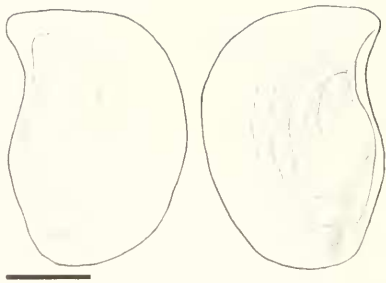


FIG. 253. Operculum of *Alcadia hojarasca*, paratype, ZMB 103387; scale bar 0.5 mm.



FIG. 254. Radula of *Alcadia hojarasca*. A. Comb-lateral. B. Marginals; scale bar 50 μ m.



FIG. 255. Female reproductive system of *Alcadia hojarasca*, IR 1242; scale bar 0.5 mm.

the species renders it impossible to recognize mature specimens without closer anatomical studies of the individuals. Furthermore, whether or not mature specimens still increase in shell size remains an unanswered question.

Habitat

Alcadia hojarasca is a ground dweller, it was only found under and between leaves in different stages of decay. The species appears to have a preference for *Cecropia*-leaves. This observation was also made by Zaidett Barrientos for *A. boeckeleri*.

Distribution (Fig. 256)

The species is only known from the type locality and adjacent areas. It is found on the higher elevations of the northeastern slope of the Cordillera de Tilarán.

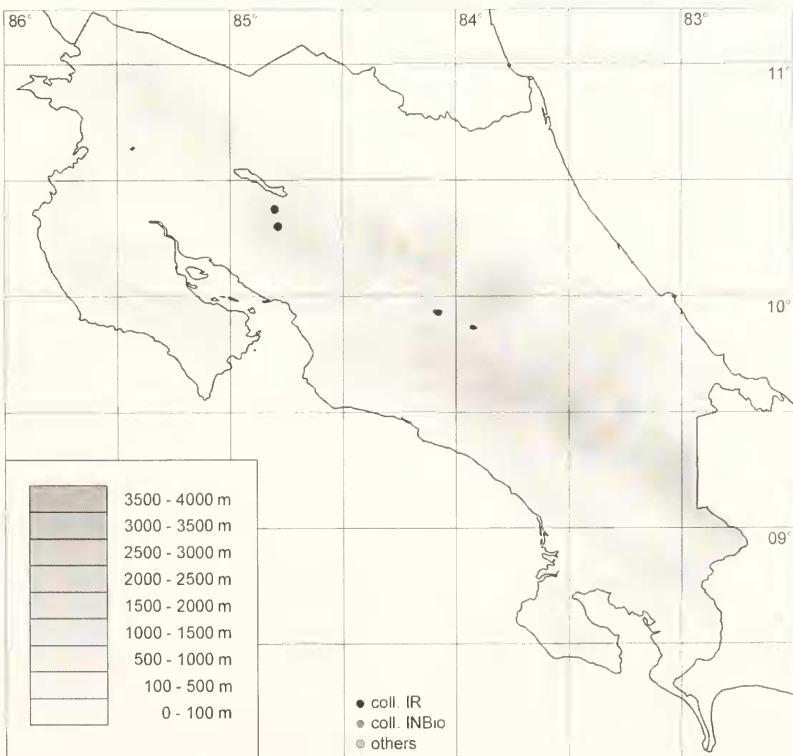


FIG. 256. Records of *Alcadia hojarasca* in Costa Rica.

Discussion

On the Central American mainland there are no other known species of this size that have periostracal hairs persisting in adult stage. The only species with a hairy periostracum on the mainland belong to the genus *Schasicheila*, which is easily characterized by the protruding edges of the operculum, a different embryonic shell structure, and great differences in the female reproductive system (see below).

The only Central American species comparable in size or probably shape is *Helicina exigua* L. Pfeiffer, 1849, described from Honduras. But in the original description, there is no hint given as to periostracal hairs. The surface is described as "subtilissime punctato-striatula", but even eroded periostracal hairs would not leave punctulations because they originate from projections of periostracal folds. Furthermore, *H. exigua* has never been illustrated, and it is treated by von Martens (1891) as a dubious species.

It is rather unusual for helicids or snails in general not to have a distinctly developed or at least thickened outer lip at the aperture as a sign of maturity and not to further grow in size. In fact, this species looks somewhat immature. On the one hand, field collections revealed specimens of different sizes but even the biggest specimens did not display a differentiated aperture. But on the other hand, dissections of specimens of about the same size as the type have shown that the reproductive system is fully developed, and in the female's receptacula seminis sperm is present, as it is in the male's vas deferens. So there is strong evidence to suggest that the specimens described above represent the adult stage, although it cannot be determined in the case of every individual if it already has reached maturity, because a normal size variation combined with sexual dimorphism still have to be taken into consideration.

For comparison with *Alcadia boeckeleri*, refer to that species.

Alcadia (Microalcadia) boeckeleri
(Richling, 2001)

Helicina boeckeleri Richling, 2001: 6–7 (text figure)

Type Material

Holotype: INBio 3404980, male (leg. I. Richling, 12.3.2000)

Paratype 1: ZMB 103388, female (same data as holotype)

Dimensions (height/greatest diameter):

Holotype: 2.2/2.6 mm

Paratype 1: 2.3/2.7 mm

Type Locality

NW-Costa Rica, Guanacaste Province, Parque Nacional Guanacaste, about 10 km S of Santa Cecilia, Volcán Orosí, near field station Pitilla, 10°59'18"N, 85°25'34"W, 700 m a.s.l., beginning of Sendero Orosilito, primary forest.

Examined Material

INBio COLLECTION

Guanacaste: *Parque Nacional Guanacaste, La Cruz, 9 km S de Santa Cecilia, Estación Pitilla*: 10°59'25"N, 85°25'38"W, 700 m a.s.l.: leg. malacological staff of INBio, 01.03.1995: 9 spec. (INBio 1498481); leg. Evelio Alfaro, 19.04.1995: 1 spec. (INBio 1483310); 10°59'33"N, 85°25'46"W, 700 m a.s.l.: leg. Dunia Garcia, 10.08.1995: 1 ad. (INBio 1488038); 7 ads., 1 s.ad. (INBio 1488068); *Sector Finca Nacho*, 10°58'43"N, 85°25'49"W, 700 m a.s.l.: leg. C. Moraga, 18.08.1994: 1 ad. (INBio 1480339); *Sendero Mena*, 10°59'27"N, 85°25'49"W, 700 m a.s.l.: leg. malacological staff of INBio, 01.06.1993: 6 spec. (INBio 1466290); *Sendero Los Memos*, 11°02'00"N, 85°25'20"W, 700 m a.s.l.: leg. Calixto Moraga, 02.04.1995: 1 spec. (INBio 1482793)

Etymology

The species is dedicated to Dr. Wolfgang Böckeler who first introduced me to Costa

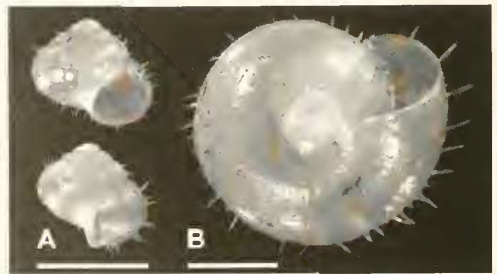
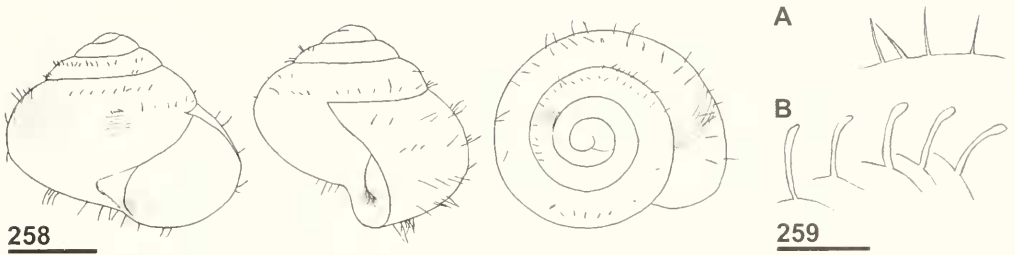


FIG. 257. *Alcadia boeckeleri*. A. Holotype, INBio 3404980, height 2.2 mm. B. Paratype, ZMB 103388; scale bar 2.5 mm (A), 1 mm (B).



FIGS. 258, 259. *Alcadia* spp. FIG. 258. *Alcadia boeckeleri*, holotype, INBio 3404980, height 2.2 mm. FIG. 259. Periostracal hairs of A. *Alcadia boeckeleri*, INBio 3404980. B. *Alcadia hojarasca*, INBio 3404979; scale bar 1 mm (Fig. 258), 0.5 mm (Fig. 259).

Rica and subsequently so often joined me in my search for the hidden helicínids.

Description

Shell (Figs. 257, 258, 336P): Very small, globose and fragile. Color yellowish-brown. Embryonic shell with about 1 whorl, without clearly marked transition into adult shell; subsequent whorls about 3, regularly increasing in size. Surface with fine spiral cords that are

axially crossed by very fine threads. On last whorl, 5 rows of periostracal hairs; on previous whorls the upper 2 rows are present. Hairs thin and at the end sharpened (Fig. 259A). Basal callus weakly developed and near columella granulated. Aperture oblique, rather straight. Outer lip undifferentiated from whorl, appearing as not fully grown.

Internal Shell Structures: Could not be investigated.



FIG. 260. Teleoconch surface structure of *Alcadia boeckeleri*, 1st whorl; scale bar 100 μ m.



FIG. 261. Embryonic shell of *Alcadia boeckeleri*; scale bar 100 μ m.

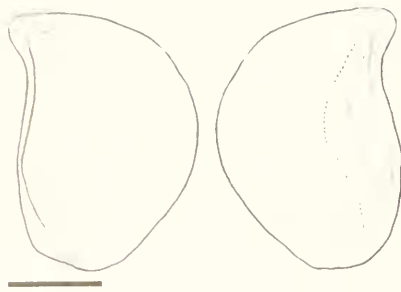


FIG. 262. Operculum of *Alcadia boeckeleri*, holotype, INBio 3404980; scale bar 0.5 mm.

Teleoconch Surface Structure (Fig. 260): A zone of transitional structure of about $\frac{1}{3}$ of a whorl, closely resembling oblique diverging grooves, is continued by numerous spiral cords, crossed only by growth lines.

Embryonic Shell (Fig. 261): The embryonic shell surface structure is similar to that of *Alcadia hojarasca*. Diameter: 488 μm ($n = 1$).

Operculum (Fig. 262): Thin, only slightly calcified, calcareous plate only covering the central area. Columellar margin irregularly S-shaped, upper edge acute, but rounded, at lower edge columellar margin continuously changing into outer margin. Nearly transparent, whitish-amber colored. Inner side with a little ridge parallel to the columellar margin.

Animal (Fig. 339G): The color is similar to *Alcadia hojarasca*.

Radula: The radula of *Alcadia boeckeleri* could not be investigated, because sufficient material was lacking.

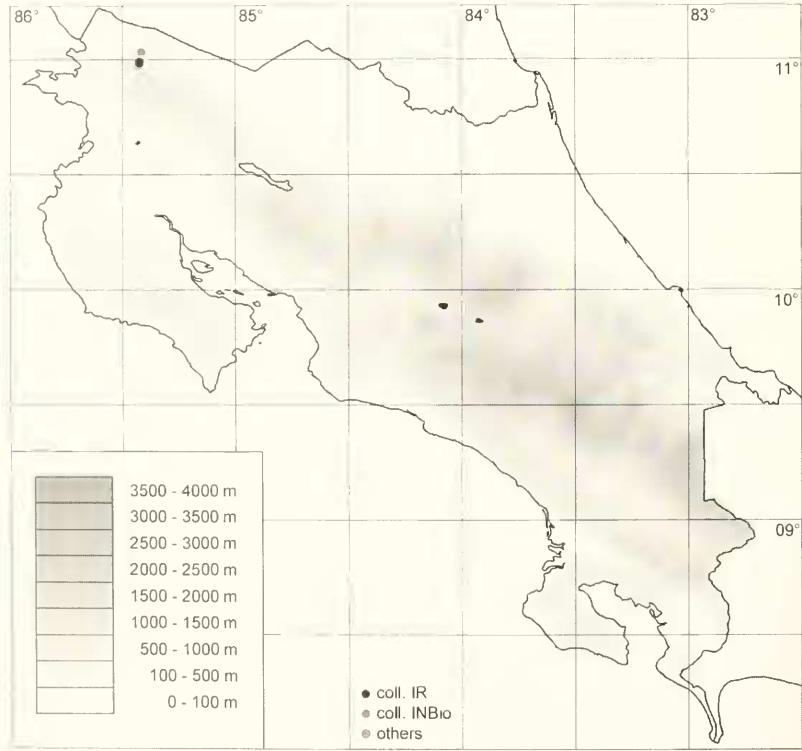


FIG. 263. Records of *Alcadia boeckeleri* in Costa Rica.

Female Reproductive System: The inspection of a single female revealed similar structures as in *Alcadia hojarasca*.

Morphometry and Sexual Dimorphism

See *Alcadia hojarasca*.

Habitat

The species is a typical ground dweller that lives in the leaf litter. See also under *Alcadia hojarasca*.

Distribution (Fig. 263)

The species is only known from the area of the type locality located on the northeastern slope of the Cordillera de Guanacaste, which, together with the volcano Orosí, forms the northern limit of this mountain chain.

Discussion

For general discussion, see *Alcadia hojarasca*.

Alcadia boeckeleri differs from *A. hojarasca* in bearing five instead of four rows of periostomal hairs. Furthermore, the hairs are much thinner and they have a different shape towards the end (Fig. 259). The spire is a little more elevated in *A. boeckeleri*.

Lucidella lirata
(L. Pfeiffer, 1847)

Helicina lirata L. Pfeiffer, 1847a: 150 (not figured)

Helicina lirata – L. Pfeiffer, 1847b: 153

Helicina lirata – L. Pfeiffer, 1848: 83

Helicina unidentata – L. Pfeiffer, 1848: 83 [without description]

Helicina unidentata L. Pfeiffer, 1849: 125 (not figured): Honduras (Dyson, coll. Cuming)

Helicina rusticella Morelet, 1849: 21 (not figured): Island Carmen

Helicina lirata – L. Pfeiffer, 1850: 1415, pl. 4, figs. 40–43: Mexico: Yucatan (Hegewisch)

Helicina unidentata – L. Pfeiffer, 1850: 14, pl. 9, figs. 14–17

Helicina lirata – L. Pfeiffer, 1852a: 341

Helicina unidentata var. – L. Pfeiffer, 1852a: 341

Helicina unidentata – L. Pfeiffer, 1852a: 341

Helicina lirata – L. Pfeiffer, 1852b: 246

Helicina unidentata var. – L. Pfeiffer, 1852b: 246

Helicina unidentata – L. Pfeiffer, 1852b: 246

Helicina lirata – L. Pfeiffer, 1856b: 236: Mexico: Chiapa (Ghiesbreght)

Helicina lirata – von Martens, 1860: 59: Venezuela: near Maracaybo or environs of Merida

Helicina lirata – Tristram, 1864: 413: Guatemala: mountain-forests of Vera Paz (Salvin)

Helicina lirata – von Martens, 1865: 67

Helicina semistriata Sowerby, 1866: 281, pl. 268, fig. 86

Helicina unidentata – Sowerby, 1866: 281, pl. 268, fig. 87

Helicina lirata – Sowerby, 1866: 281, pl. 268, figs. 88–89

Helicina lirata – Bland, 1866: 8

Helicina unidentata – Bland, 1866: 8

Helicina (Perenna) lamellosa Guppy, 1867: 260, pl. X, fig. 4: Trinidad: Gulf of Paria, islet Cotoras

Helicina semistriata – Tate, 1870: 159: Nicaragua: in the woods and coconut groves about Boca del Toro, region Chontales [area around Acopapa, NE of Lago de Nicaragua]

Helicina lirata – Strebel, 1873: 21, pl. 1, fig. a, pl. 2 fig. 8: Mexico: Bajadas, Veracruz and near Antigua

Helicina lirata – von Martens, 1873: 56: Venezuela

Helicina lirata – Reeve, 1874: pl. 14, fig. 121

Helicina unidentata – Reeve, 1874: pl. 14, fig. 122

Helicina lyrata [sic] – Angas, 1879: 484: Costa Rica (Gabb)

Helicina unidentata – Ancey, 1886: 254: Honduras: Ile d'Uitilla (Dyson, Simpson)

Lucidella lirata – Jousseaume, 1889: 232, 235, 256: Venezuela: Caracas, San-Esteban

Helicina lirata – von Martens, 1891: 4142, pl. I, fig. 18 (living animal): E-Mexico: Vera Cruz, at the "bajadas"; S-SE-Mexico: Chiapas, Teapa and San Juan Bautista in Tabasco; Yucatan; N-Guatemala: mountain forests of Vera Paz; S-Guatemala: Retalhuleu; Venezuela

Helicina lirata var. *rusticella* – von Martens, 1891: 41: Yucatan: Island of Carmen, in the Gulf of Campeche

Helicina lirata var. *unidentata* – von Martens, 1891: 41: Honduras; 607: Honduras: Utila Island

Helicina lirata var. *semistriata* – von Martens, 1891: 41: N-Panama: Boca del Toro, Chiriqui

- Helicina lirata* – Pilsbry, 1891: 332: Mexico: N-Yucatan: Labna; Honduras: Utilia Island (Simpson)
- Helicina (Poenia) lirata* – Fischer & Crosse, 1893: 397–399: same data as von Martens, 1891 (for *H. lirata* and *H. lirata* var. *unidentata*) and Mexico: Yucatan, Labna
- Helicina (Poenia) lirata* var. *rusticella* – Fischer & Crosse, 1893: 397–399: same data as von Martens, 1891
- Helicina (Perenna) lamellosa* – Guppy, 1893: 228
- Helicina (Helicina Perenna) lirata* – Guppy, 1895: 74
- Helicina (Helicina Perenna) semistriata* – Guppy, 1895: 74
- Helicina (Helicina Perenna) lamellosa* – Guppy, 1895: 74
- Helicina lirata* – von Martens, 1900: 607: S.E. Mexico: San Juan Bautista, garden of the Juarez Institute in the same town; Yucatan: Labna; N-Guatemala: Panzos; SW-Costa Rica: Alto de Mano Tigre, 690 m [not localized] (Pittier)
- Helicina lirata* var. *rusticella* – von Martens, 1900: 607: SW-Costa Rica: El Pozo, in the shingle (gravices) of the Río Grande de Terraba [not localized: Palmar Norte: 08°57'N, 83°27'W, Puntarenas Province] (Pittier)
- Helicina lirata* – Pilsbry, 1904: 782: Mexico: Veracruz: Antigua (Rhoads)
- Helicina lirata* – Pilsbry, 1910: 503: Panama: Canal Zone: Tabernillo (Brown)
- Lucidella lirata* – Wagner, 1911: 341, pl. 68, figs. 5–7: S-Mexico, Guatemala, Honduras, Venezuela
- Lucidella lirata lamellosa* – Wagner, 1911: 341342, pl. 68, fig. 4: Trinidad (island)
- Lucidella (Perenna) lirata* – Pilsbry & Brown, 1912: 585
- Lucidella lirata* var. *lamellosa* – Vernhout, 1914: 26–27: Suriname: Environs of Paramaribo
- Lucidella lirata* – Hinkley, 1920: 41, 49, 52: Guatemala: Livingston; Jocolo plantation on north side of Lake Isabal: lake drift; Alta Verapaz: Chama between Río Tsalbha and Río Negro: also river drift
- Lucidella (Poenia) lirata* – Baker, 1922a: 54–55, pl. III, fig. 5, pl. V, fig. 21 (radula): Mexico-Venezuela; Mexico: Tabasco: San Juan Bautista: Garden of Juarez Institute (Rovirosa)
- Lucidella (Poenia) lirata* – Baker, 1922b: 36: Mexico: S Vera Cruz, near hacienda de Cuatolapam (Río San Juan – Arroyo Hueyapam, canton of Acayacan (Michigan-Walker-Expedition)
- Lucidella (Poenia) lirata* – Baker, 1923: 22–23: Venezuela: San Esteban, Palma Sola, Aroa, Estación Táchira, La Fria (Michigan-Williamson-Expedition)
- Lucidella lirata* – Pilsbry, 1926a: 59, 71: Panama: Canal Zone: Tabernilla (Brown), near Darien and Juan Mina (Zetek), Panama City and Taboga Island (Zetek), Bocas del Toro (Gabb)
- Lucidella lirata* – Pilsbry, 1926b: 127: Costa Rica: Cahuita [09°44'01"N, 82°49'48"W] (Olsson)
- Lucidella (Poenia) lirata* – Baker, 1928: 33–34, pl. II, figs. 9–11 (female reproductive system): Mexico: Veracruz: Atoyac, 1300–1475 feet
- Lucidella lirata* – Pilsbry, 1930: 339: Panama: Canal Zone: roadside in SE of Empire; Taboga Island (Pinchot-Expedition)
- Lucidella (Poenia) lirata* – Bequaert & Clench, 1933: 543: Mexico: Yucatan, Chichen Itzá
- Lucidella lirata* – Goodrich & van der Schalie, 1937: 12, 14–16, 33: Guatemala: Petén: region of headwater of Río San Pedro de Mártir, lower Río de la Pasión; Alta Verapaz: upper part of Río de la Pasión
- Lucidella lirata* – Richards, 1938: 176: Honduras
- Lucidella lirata* – Richards & Hummelinck, 1940: 12–13: Venezuela: Margarita Island: Hills SE La Asunción; Cerro del Piache; just above El Valle; La Sierra, El Valle; Toma de Agua del Valle; Toma de Agua de Encañado, San Juan; Los Vagras; between Los Vagras and coast
- Lucidella lirata* – Bequaert, 1957: 208: Mexico: Chiapas: Selva Lacandona: Laguna Ocotal, 950 m, Laguna Ocotal to El Censo, 1,000 m; Veracruz, Tabasco, Yucatan, Quintana Roo, Guatemala to Panama
- Lucidella lirata lamellosa* – Bequaert, 1957: 208
- Lucidella lirata* – Basch, 1959: 8: Guatemala: Petén: Tikal National Park, 17°10'N, 89°25'W
- Lucidella lirata* – Hubricht, 1960: 83: USA: S-Texas: beach drift
- Lucidella (Poeniella) lirata* – Haas & Solem, 1960: 130: British Honduras [Belize]: Río Frio Cave, Cayo District
- Lucidella lirata* – Branson & McCoy, 1963: 102–103: Mexico: Campeche: Airport, Ciudad del Carmen

Lucidella lirata – Thompson, 1967: 228229:
Mexico: Campeche: 8.1 mi SW Champotón,
5.1 mi NNW Dzibalchén, 4.9 mi W
Hopelchén, 3.4 mi S Cayál (19°45'N,
90°10'W), 7.2 mi S Pixtún, 10.2 mi E
Escárcega, 19.2 mi E Silvituc; Quintana
Roo: 4 mi E Xpujil, 7.1 mi NNW Xiatil

Lucidella lirata – Regteren Altena, 1974: 71:
Suriname

Lucidella lirata – Tillier, 1980: 35, 36, figs. 20,
21 (operculum): French Guiana: Aouara,
Saut Sabbat (Abattis)

Lucidella (Poenia) lirata – Thompson, 1982:
fig. 13 (radula), 27–28 (embryonic shell)

Lucidella lirata – Monge-Nájera, 1997: 113:
Costa Rica

Synonymy

Helicina unidentata L. Pfeiffer, 1849

Helicina rusticella Morelet, 1849

Helicina semistriata Sowerby, 1866

Helicina lamellosa Guppy, 1867

Original Description

"T. orbiculato-conoidea, tenuis, acute et
confertim concentrice lirata, diaphana, albida;
spira conoidea, acuta; anfr. 4,5–5 vix
convexusculi, ultimus carinatus, basi medio
impressus; apertura obliqua, rotundato-
subtriangularis; columella brevissima, sim-
plex, in callum basalem tenuissimum dilatata;
perist. breviter expansum, margine basali
medio obsolete unidentato.

Diam. 4, alt. 2 $\frac{2}{3}$ mill.

Habitat in Mexico, Yucatan (Hegewisch)."

Type Material

Not located (assumed to be in the collection
of L. Pfeiffer, because it was not otherwise
stated, collection L. Pfeiffer having been most
likely destroyed in Stettin Museum, Poland
during World War II).

Type Locality

"Mexico, Yucatan" [not clear, whether it re-
fers to the Mexican State of Yucatán or the
Mexican part of the peninsula of Yucatán].

Examined Material

LEG. I. RICHLING

Limón: *Parque Nacional Cahuita*, trail from
Cahuita to Puerto Vargas, coastal forest with

coco palms: about 09°43'27"N, 82°50'28"W,
4 m a.s.l.: 02.03.1998: (IR 418); 10.03.1999:
(IR 756); 08.08.1999: (IR 902); 10.08.1999:
(IR 913); 04.03.2000: (IR 1314); (IR 1316);
14.03.2001: (IR 1558); (IR 1559); (IR 1640)
Refugio Nacional de Fauna Silvestre
Gandoca-Manzanillo, S *Manzanillo*, trail
along coast line to S, coastal forest, about
09°38'06"N, 82°38'26"W, 50 m a.s.l.,
14.09.1999: (IR 1098); (IR 1124)

W *Liverpool*, Mexico, at Río Blanco, high
water deposit, 09°58'32"N, 83°08'32"W, 35
m a.s.l.: 22.02.1997: (IR 7); 12.03.1997: (IR
113)

N *Shiroles*, along Quebrada Kirio,
09°35'38"N, 82°57'20"W: 120 m a.s.l.:
15.03.1997: (IR 162); 60 m a.s.l.:
03.03.1998: (IR 435)

W *Bribri*, road to Uatsi, about 09°38'11"N,
82°51'48"W, 30 m a.s.l.: at crossing with Río
Carbón, 30 m a.s.l.: 17.3.1997: (IR 187);
wooded valley within banana plantation, 50
m a.s.l.: 15.3.2001: (IR 1586)

Southern road from *Bribri* to *Shiroles*, small
banana plantation near creek, 09°35'17"N,
82°52'46"W, 50 m a.s.l., 15.03.1997: (IR
171)

Puntarenas: *Refugio Nacional de Fauna
Silvestre Golfito*, rain forest, 08°39'26"N,
83°10'50"W, 100 m a.s.l., 14.02.1999: (IR
568)

INBio COLLECTION

Limón: *Parque Nacional La Amistad*,
Quebrada Cachabri (toma de agua),
09°29'29"N, 82°59'37"W, 360 m a.s.l., leg.
Gerardina Gallardo, 26.11.1996: 3 spec.
(INBio 1488249)

*Reserva Indígena Talamanca: 1 km SW de la
Iglesia de Amubri*, 09°30'37"N, 82°57'36"W,
70 m a.s.l.: 19.10.1996: 8 spec. (INBio
1488235); 500 m E de la Iglesia de Amubri,
09°31'06"N, 82°56'50"W, 70 m a.s.l.:
21.10.1996: 6 spec. (INBio 1488268); *Sector
Amubri*, 09°30'53"N, 82°57'19"W, 70 m a.s.l.:
29.11.1994: 1 spec. (INBio 1483399);
30.11.1994: 1 spec. (INBio 1483446); 2 spec.
(INBio 1483447); 1 spec. (INBio 1483449); 6
spec. (INBio 1483450); 24.10.1996: 30 spec.
(INBio 1487958); 27.11.1996: 1 spec. (INBio
1487352); *Amubri*, Sendero Soki,
09°30'53"N, 82°57'19"W, 70 m a.s.l.:
27.11.1996: 1 spec. (INBio 1487364); 11
spec. (INBio 1488219); 11 spec. (INBio
1493414); *Suirí*, orillas del Río Telire,
09°33'56"N, 82°55'50"W, 30 m a.s.l.:
25.11.1996: 17 spec. (INBio 1487345) (all

leg. Gerardina Gallardo); *Sector Miramar, Senderos a Río Moin*, 09°37'44"N, 83°00'32"W, 150 m a.s.l.: leg. Zaidett Barrientos, 08.11.1994: 4 spec. (INBio 1475236)

1 Km S de Punta Cocles, 09°38'17"N, 82°43'25"W, 40 m a.s.l., leg. Zaidett Barrientos, 20.08.1996: 1 spec. (INBio 1487843)

Refugio Nacional de Vida Silvestre Gandoca-Manzanillo: *Sector Gandoca*, 09°35'30"N, 82°36'13"W, 0 m a.s.l.: 29.07.2000: 4 spec. (INBio 3091175); *Sector Gandoca, Camino a Gandoca*, 09°38'04"N, 82°38'37"W, 10 m a.s.l.: 28.04.2000: 5 spec. (INBio 3097927); *Sector Manzanillo, Sendero a Gandoca*, 09°38'20"N, 82°39'03"W, 2 m a.s.l.: 30.03.2000: 1 spec. (INBio 3098034) (all leg. Alexander Alvarado Mendez)

Parque Nacional Cahuita: Sector Puerto Vargas, 09°43'38"N, 82°49'09"W, 0 m a.s.l.: leg. Alexander Alvarado Mendez, 31.08.1999: 1 spec. (INBio 3091727); 4 spec. (INBio 3091733); *Sendero del límite W del parque*, 09°44'00"N, 82°50'25"W, 10 m a.s.l.: leg. malacological staff of INBio, 11.06.1997: 1 spec. (INBio 1488171)

Reserva Indígena Tayni: Sendero Tepezcuintle, 09°40'22"N, 83°01'46"W, 180 m a.s.l.: 22.04.1999: 1 spec. (INBio 3096423); *Sendero Bobocara*: 09°40'28"N, 83°02'17"W, 260 m a.s.l., 01.06.1999: 1 spec. (INBio 1498178); 09°40'28"N, 83°02'12"W, 200 m a.s.l., 01.06.1999: 7 spec. (INBio 1498248) (all leg. Alexander Alvarado Mendez)

Reserva Biológica Hitoy Cerere: Sendero Tepezcuintle: 09°40'22"N, 83°01'40"W, 140 m a.s.l., 25.04.1999: 3 spec. (INBio 1497566); 100 m a.s.l., 07.06.1999: 4 spec. (INBio 3096478); 09°40'18"N, 83°01'43"W, 140 m a.s.l., 28.04.1999: 1 spec. (INBio 1497840); *Sendero Bobócara*, 09°40'20"N, 83°03'12"W, 620 m a.s.l.: 14.06.1999: 3 spec. (INBio 3095831) (all leg. Alexander Alvarado Mendez); *Sendero Toma de Agua*, 09°40'31"N, 83°01'36"W, 100 m a.s.l.: 19.04.1994: 1 spec. (INBio 1473669); 2 spec. (INBio 1473674); 58 spec. (INBio 1474306); 30 spec. (INBio 1474336); 20.04.1994: 1 spec. (INBio 1473613) 1 spec. (INBio 1473838); 08.09.1994: 49 spec. (INBio 1475430); 70 spec. (INBio 1475444) (all leg. Zaidett Barrientos); 28.02.1994: 4 spec. (INBio 1476129);

17.07.1994: 70 spec. (INBio 1478443); 30 spec. (INBio 1478459); 06.12.1994: 2 spec. (INBio 1475673) (all leg. Gerardo Carballo); *Estación Hitoy Cerere*, 09°40'35"N, 83°01'36"W, 100 m a.s.l.: leg. malacological staff of INBio, 15.11.1993: 7 spec. (INBio 1463364); *Sendero Chato*, 09°40'41"N, 83°01'26"W, 100 m a.s.l.: leg. Marianella Segura, 17.07.1994: 10 spec. (INBio 1478236); 70 spec. (INBio 1478239)

400m NE de la Estación de Hitoy Cerere, Sendero la "Finca", 09°40'35"N, 83°01'26"W: 150 m a.s.l.: 20.07.1999: 2 spec. (INBio 1495436); 110 m a.s.l.: 07.05.1999: 3 spec. (INBio 3300038); 27.09.2000: 1 spec. (INBio 3091795) (all leg. Alexander Alvarado Mendez)

Isla Uvita: frente al muelle de Limón, 09°59'45"N, 83°00'50"W, 5 m a.s.l.: leg. Alexander Alvarado Mendez, 11.10.2000: 21 spec. (INBio 3315375); 3 spec. (INBio 3315385); *lado N*, 09°59'50"N, 83°00'46"W, -10 to 5 m a.s.l.: leg. A. Berrocal, 06.05.2000: 21 spec. (INBio 3396974)

Puntarenas: Playa Blanca, 08°38'18"N, 83°26'16"W, 0 m a.s.l., leg. Guillermo Mena, 04.09.1995: 1 spec. (INBio 1479925)

Isla Pelicanos, 08°36'10"N, 83°08'48"W, 2 m a.s.l., leg. Socorro Avila, 01.11.1997: 1 spec. (INBio 3399211)

Refugio Nacional de Fauna Silvestre Golfito: Sendero Las Torres, 08°38'37"N, 83°09'54"W, 60 m a.s.l.: leg. Socorro Avila, 03.12.1997: 4 spec. (INBio 1487712); 150 m al N del Reserva, 08°39'06"N, 83°10'44"W, 40 m a.s.l.: leg. Alexander AlvaradoMendez, 14.02.1999: 3 spec. (INBio 1501379); *Extremo NW del Aeropuerto de Golfito*, 08°39'39"N, 83°11'13"W, 100 m a.s.l.: leg. Socorro Avila, 03.11.1997: 1 spec. (INBio 1487165); 3 spec. (INBio 1487172)

Parque Nacional Piedras Blancas, Playa San Josecito, 08°39'49"N, 83°15'35"W, 5 m a.s.l., leg. Eida Fletes, 27.10.1996: 2 spec. (INBio 1487318)

Quebrada Benjamin, carretera al tanque del agua 600 m del Barrio Alemania, 08°58'39"N, 83°28'19"W, 100 m a.s.l., leg. Socorro Avila, 08.05.1997: 1 spec. (INBio 1487661); 1 spec. (INBio 1487691)

Palmar Norte, Barrio Alemania, Sendero a Jalisco, 1 Km al NE del Tanque de Acueductos, 08°59'21"N, 83°28'16"W, 400 m a.s.l., leg. Socorro Avila, 08.05.1997: 2 spec. (INBio 1487736); 3 spec. (INBio 1487756)

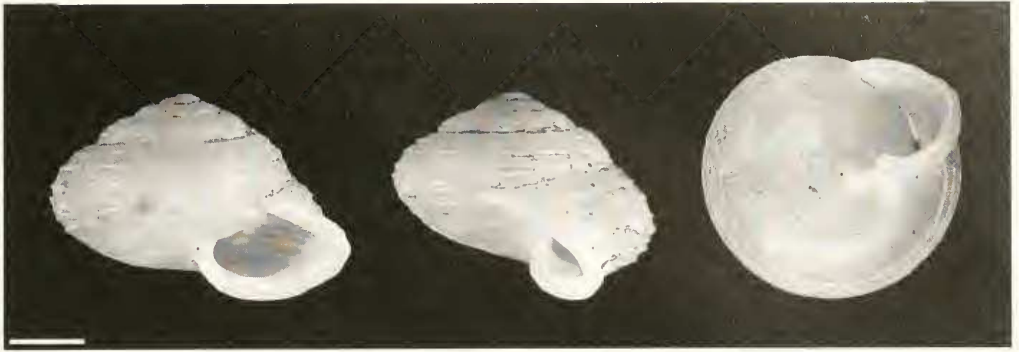


FIG. 264. *Lucidella lirata*, Cahuita, IR 1559; scale bar 1 mm.

OTHER SOURCES

COSTA RICA

Limón: Pandora [about 09°43'N, 82°58'W], leg. F.G. Thompson (FGT-100), 05.08.1964 (UF 214773)

7 km from Valle La Estrella, at Hitoy Cerere National Park [about 09°40'35"N, 83°01'36"W], 152 m a.s.l., E.L. Raiser et al. (ERL 079), 09.08.1994 (UF 41405, UF 41406); E.L. Raiser (ERL 080), 09.08.1994 (UF 41421)

1 km NW of Cahuita, 09°45.5'N, 82°50.9'W, leg. F.G. Thompson (FGT-5616), 25.02.1996 (UF 268476)

NICARAGUA

Matagalpa: 4.5 km. S of Matagalpa, 1,200 m a.s.l., leg. F.G. Thompson, 16.07.1956 (UF 127683)

Description

Shell (Figs. 264, 336Q): Orbiculate-conoidal, depressed, thin, small sized, dull. Color: dark yellowish to brown, diaphanous (whit-

ish: as in original description only faded specimens). Whorls sculptured with a varying number of close-set, prominent, sharp spiral ridges at about equal distance, upper a little wider spaced, some smaller ridges in between. Surface textured with irregular, strong growth lines crossing spiral sculpture. Embryonic shell with about 1 whorl; $3\frac{5}{8}$ –4 subsequent whorls slightly convex; last whorl rounded with a slight keel on periph-

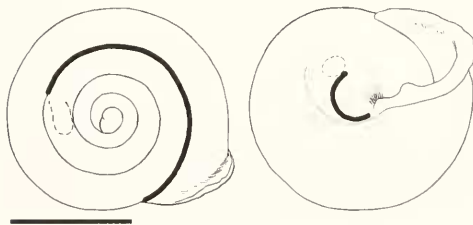


FIG. 265. Axial cleft and muscle attachments of *Lucidella lirata*, IR 1559; scale bar 2 mm.



FIG. 266. Teleoconch surface structure of *Lucidella lirata*, 2nd whorl; scale bar 100 μ m.

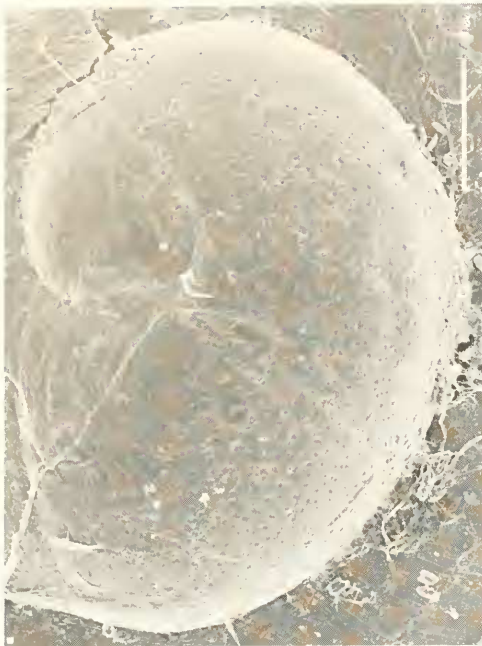


FIG. 267. Embryonic shell of *Lucidella lirata*; scale bar 100 μ m.

ery, umbilical region deeply impressed; whorls rapidly increasing in size and only slightly descending, forming a low spire and a slightly pointed apex. Suture deeply impressed. Aperture oblique and curved backwards towards its base. Outer lip of the same color as the preceding whorls, thickened and narrowly expanded, a slight notch at insertion to body whorl. Reflection very narrow, lower palatal margin with a broad

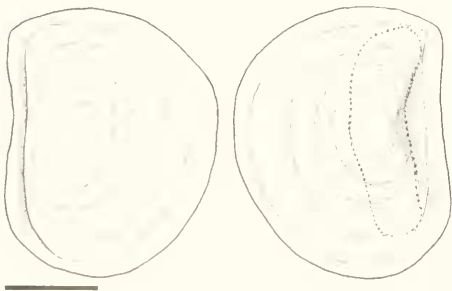


FIG. 268. Operculum of *Lucidella lirata*, IR 1559; scale bar 0.5 mm.

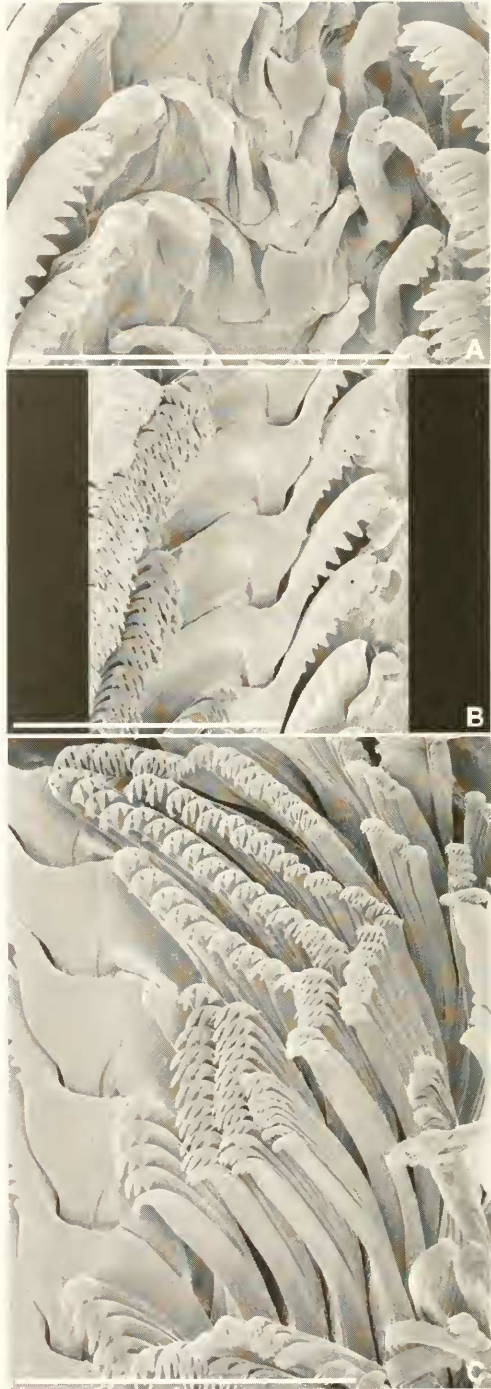


FIG. 269. Radula of *Lucidella lirata*. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 μ m.

tooth that is more or less well developed. Columella short. Basal callus weakly developed and granulated.

Internal Shell Structures (Fig. 265):

Teleoconch Surface Structure (Fig. 266): A transitional pattern is absent, the teleoconch is structured with the typical spiral ridges throughout, the interspaces are smooth except for fine growth line.

Embryonic Shell (Fig. 267): Contrary to the pitted embryonic shells described for species of *Helicina*, the pits of *Lucidella lirata* are not arranged in distinct spiral lines. The interspacial distance exceeds the diameter of the pits, which are more sparsely scattered over the surface. The embryonic shell is even smaller than in the smaller species *Alcadia hojarasca* and *A. boeckeleri*. Diameter: 426 μm (± 12) (408–465) ($n = 13$) (IR 756, IR 1314).

Operculum (Fig. 268): Outer surface very slightly calcified, a noticeable ridge only at the columellar side, which is quite straight. Color horny-amber and transparent.



FIG. 270. Female reproductive system of *Lucidella lirata*, IR 1314; scale bar 0.5 mm.

Nucleus at a significant distance from the columellar margin. Shape broadly ovoid and only truncated towards the columella.

Animal (Fig. 339H): Only the tentacles are grey, the rest of the body is whitish-yellow. The mantle may be spotted grey, but this is only visible in individuals removed from their shell.

Radula (Fig. 269): A-central elongated and smooth; B- and C-central each bearing about 5–6 cusps. Comb-lateral with 9–12 cusps, cusps on marginals slowly increasing in number. Total number of rows was not counted. Baker (1922a) and (Thompson, 1982) found fewer cusps on the comb-lateral.

Female Reproductive System (Fig. 270): The receptaculum seminis between the two limbs of the V-organ is not developed; it is replaced by an accessory sperm sac on the top of the V-organ or the very beginning of the descending limb respectively, but it is located on the outside of the V-organ. The bursa copulatrix is relatively small and without any lobes. In contrast, the distal side of the provaginal sac is deeply lobed, an additional lobule may occasionally be developed on its stalk. The bursa copulatrix enters the reception chamber via the stalk of the provaginal sac rather than directly. The provaginal duct that continues from the stalk of the provaginal sac is very short and slender. The pallial oviduct is much less folded than in the species of *Helicina*. It receives an additional sac a short distance from the reception chamber, which serves for sperm storage.

The anatomy of the species has already been studied by Baker (1928), but, according to his studies of *Lucidella aureola* (Férussac, 1822), he assumed the existence of a receptaculum seminis as described above for the species of *Helicina* (he had only a single specimen and "it was broken away ..."). The study of serial sections excludes the presence of such an organ. Furthermore, the additional sac on the oviduct escaped Baker's attention.

Morphometry and Sexual Dimorphism (Table 14, Fig. 271)

Sufficient numbers of specimens were found only at Cahuita. Because morphological differ-

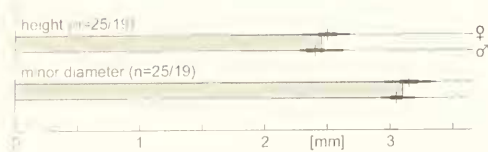


FIG. 271. Measurements of *Lucidella lirata* according to Table 14; on each line: mean value, standard deviation, absolute range; number of individuals given as "n = females/males"; upper line: females, lower line: males; in between and shaded: average of both.

ences between populations cannot be considered here, only height and minor diameter were measured.

The values of males and females widely overlap (Fig. 272), so that statements based on very few shells will only be correct by coincidence (Baker, 1928: 1 female > a few males). On average, females are larger than males. In interpolation from the minor diameter, the males have an average volume of about 92.5% of that of the females, thereby representing the smallest degree of sexual dimorphism found among Costa Rican species of Helicinidae.

Habitat

Lucidella lirata is a typical ground dweller, living in the leaf litter under and between decaying leaves, trunks and fruits. In Costa Rica, it was found abundantly very close to the sea shore in a coconut palm forest on sandy gravel bottom. A semiaquatic behavior (in and at edge of pools, often together with aestivating *Pisidium* and *Planorbis*) described by Baker (1922b) for populations in southern Vera Cruz, Mexico, was not observed. Besides mesic and rain forests, Thompson (1967) also mentions a constantly wet swampy area in Campeche, Mexico as habitats of *L. lirata*.

Distribution

Lucidella lirata is very widespread in Central America. It ranges from southern Mexico to Panama and along the northern coast of South America, where it is found in Venezuela, French Guyana, and Suriname. It inhabits some coastal islands, such as Isla de Utila, Honduras, and Isla de Margarita and Trinidad, Venezuela, but it is absent from the southern

Lesser Antilles. In Mexico, *L. lirata* seems to be restricted to the southeastern states Veracruz, Chiapas, Campeche, Quintana Roo, and Yucatán, although it may be rare towards the extreme tip of the Peninsula de Yucatán, because it was only recorded twice from the latter state (Labna and Chichen Itza). According to Correa-Sandoval (2000), it has not been reported north of Jalapa in central Veracruz.

The records for Costa Rica (Fig. 273) are concentrated in two regions, the southern Pacific and the Caribbean plains, but within these areas the species was found at various different sites. According to the quantity of material and the author's own field experience, *L. lirata* occurs more abundantly on the Caribbean side. The distribution stretches along the coast line, where slightly elevated areas are mainly inhabited. In Costa Rica, the species is only occasionally found on altitudes up to 620 m in Hitoy Cerere or up to 690 m in Alto de Mano Tigre on the Pacific side respectively, whereas Bequaert (1957) reported *L. lirata* up to 1,000 m in Mexico.

Discussion

Because Costa Rican populations represent only a small area within the wide distribution of *Lucidella lirata*, and because it is the only species of that genus in Costa Rica, rendering a comparison with other similar taxa within the area of the study unnecessary, it seemed appropriate to investigate and discuss the species to a lesser extent than the representatives of the genus *Helicina* and to accept the interpretations of earlier authors on this subject (e.g., synonymy). For this reason, only Costa Rican material is listed above. A comprehensive revision of the species should encompass samples from the entire area of distribution, something beyond the focus of the present study.

Lucidella lirata varies throughout its area of distribution with respect to the number of spiral ridges and their extent towards the umbilical area, for example, Venezuelan specimens show all intermediates between the typical form and *lamellosa* (Baker, 1923; Regteren Altena, 1974; Tillier, 1980). Furthermore, the elevation of the spire and the dentition of the outer lip are subject to variation. In the Costa Rican samples, the basal tooth is usually well developed, and the upper outer lip is irregularly crenulated, the spiral striation is present only on about half the distance or less from the periphery to the umbilical area.

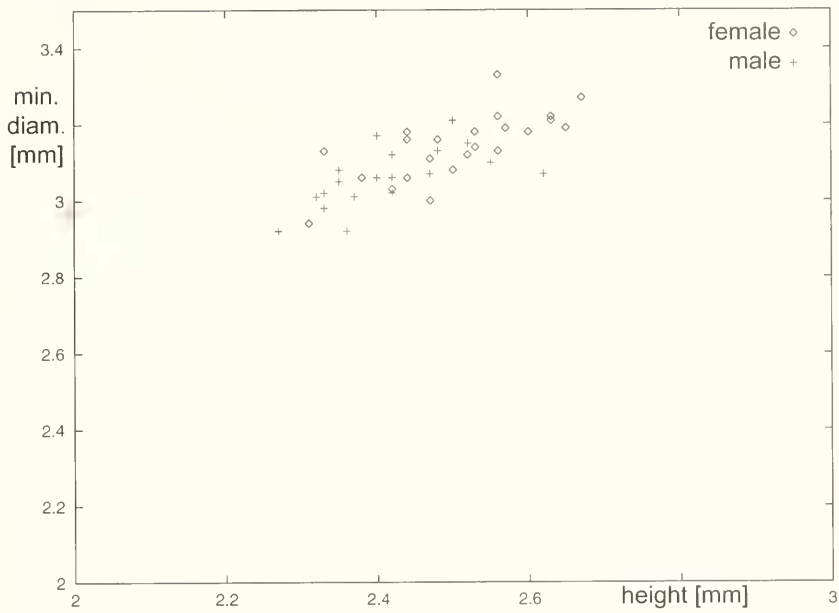


FIG. 272. Range of measurements in females and males of *Lucidella lirata* for height and minor diameter in the population from Cahuita.

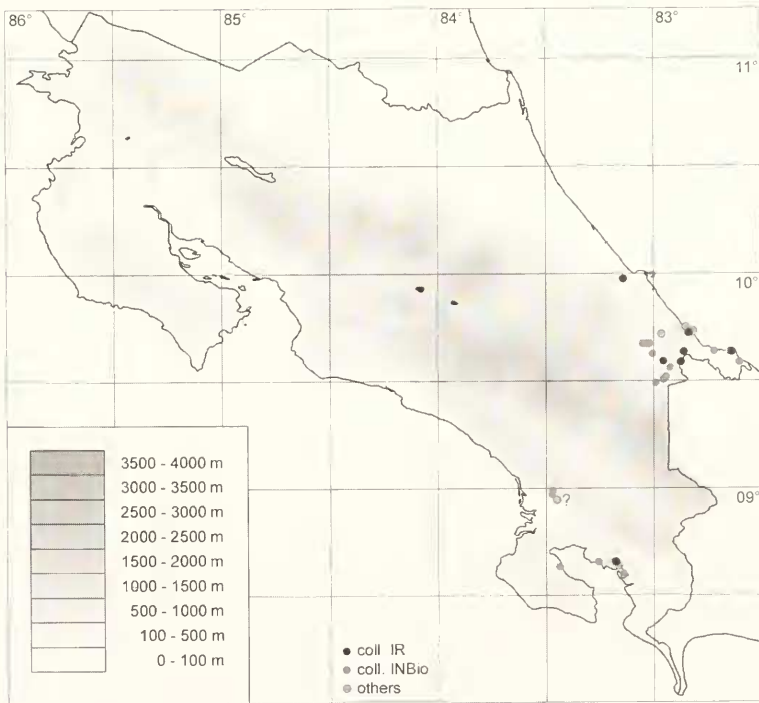


FIG. 273. Records of *Lucidella lirata* in Costa Rica.

TABLE 14. Measurements of the Cahuita-population of *Lucidella lirata* given as mean value with standard deviation, minimum and maximum value (min, max), and number of specimens (min. diam. = minor diameter); linear measurements [mm].

"Cahuita" (altitude 5–10 m) lot IR 1314						
	Sex	Mean value	Deviation	Min	Max	Number
Height	f	2.51	0.08	2.31	2.67	25
Height	m	2.41	0.07	2.27	2.62	19
Min. diam.	f	3.14	0.07	2.94	3.33	25
Min. diam.	m	3.06	0.06	2.92	3.21	19

QUESTIONABLE SPECIES FOR COSTA
RICA

Helicina (Oligyra) flavida
Menke, 1828

Examined Material (Fig. 274)

COSTA RICA

Limón: Field cleared of forest vegetation (now soccer field), adjacent to Los Corales III, Puerto Limón, 10°00'06.7"N, 83°02'37.9"W, leg. D.G. Robinson, Summer 1984: 2 ads. (dead collected) (APHIS PPQ USDA)

Distribution

The species is only known for Costa Rica from the two dead specimens collected very near Puerto Limón (Fig. 275). Otherwise, *Helicina flavida* is widely distributed in southern Mexico (states: Puebla, N- to S-Veracruz, Tabasco, Chiapas, Campeche, Quintana

Roo), northern Guatemala (departments: Petén, Alta Verapaz, Izabal) and Belize (Cayo district) (von Martens, 1890–1901; Hinkley, 1920; Baker, 1922b; Bequaert, 1957; Haas & Solem, 1960; Thompson, 1967; Correa-Sandoval, 2000).

Discussion

Helicina flavida was originally described from Jamaica, but aside from some records from the Antilles in some mid-19th century publications, almost all subsequent authors treated the Central American mainland species under this name, because a similar species had not been found on the Greater Antilles. Only Wagner (1910a) still retained the use of *flavida* for a non-existent Jamaican species and applied the younger, synonymous name *Helicina brevilabris* L. Pfeiffer, 1856 to the mainland species.

Literature records of *Helicina flavida* var. for Costa Rica (von Martens, 1890–1901) clearly referred to *H. beatrix*. Therefore, the species is newly recorded for Costa Rica, although it remains doubtful whether it still exists in Costa Rica or whether it was even indigenous to Costa Rica in the first place. Having recognized the peculiarity of his discovery, David Robinson re-examined the locality in 1998 but by then it was "totally built over by urban expansion". His examination of some other limestone spots near Puerto Limón where the limestone may have made it possible for the species to exist was unsuccessful (personal communication). On the other hand, Puerto Limón is the only Caribbean port of Costa Rica, where the enormous trade of agricultural



FIG. 274. *Helicina flavida*, Puerto Limón, APHIS PPQ USDA, height 5.9 mm, 5.1 mm; scale bar 2.5 mm.

products actually takes place and introduction of foreign species is thereby facilitated. Robinson (1999) lists *H. flavida* among those species that were occasionally imported into the United States. Until better knowledge becomes available, the Costa Rican occurrence of this species remains doubtful.

MISIDENTIFICATIONS FOR COSTA RICA

Helicina amoena
L. Pfeiffer, 1849

Helicina amoena – Monge-Nájera, 1997: 113: Costa Rica [non L. Pfeiffer, 1849] refers to *Helicina pitalensis*

See under *Helicina pitalensis*.

Helicina oweniana
L. Pfeiffer, 1849

Helicina oweniana – Monge-Nájera, 1997: 113: Costa Rica [non L. Pfeiffer, 1849] refers

to *Helicina tenuis*, *H. talamancensis*, *H. gemma* and *H. monteverdensis* n. sp.

Original Description

Helicina oweniana L. Pfeiffer, 1849: 123 (not figured); L. Pfeiffer, 1850: 40–41, pl. 7, figs. 35, 36

Type Material

BMNH 20010751: 3 syntypes, leg. Mr. Ghiesbreght, Hugh Cuming coll. (in original description "Ghiesbreght")

The three syntypes (Fig. 276) are very similar to each other. Compared to most of the Costa Rican species the shells are solid. They are of whitish-yellow color with a very slight touch of green, the lower margin of the suture is whitish; the apex is red; only the outer lip is bright orange. The upper whorls are very straight; the suture very little impressed, whorls regularly descending and extending in size. Aperture oblique, outer lip

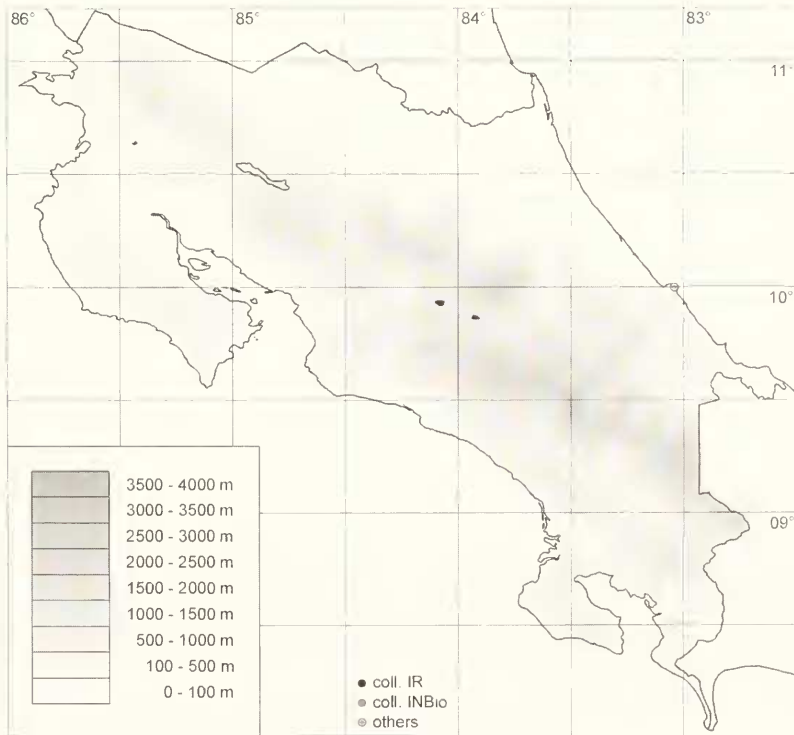


FIG. 275. Records of *Helicina flavida* in Costa Rica.

straight and perpendicularly and flatly expanded, thickened, basal margin with only a little notch. At the columella, a little groove.

Dimensions:

8.3/7.6/8.4/7.1/5.1/5.9/6.6 mm

8.5/7.9/8.6/7.2/5.3/6.2/6.8 mm

8.2/7.4/8.1/6.8/5.2/6.0/6.7 mm

Type Locality

"Chiapas, Mexico".

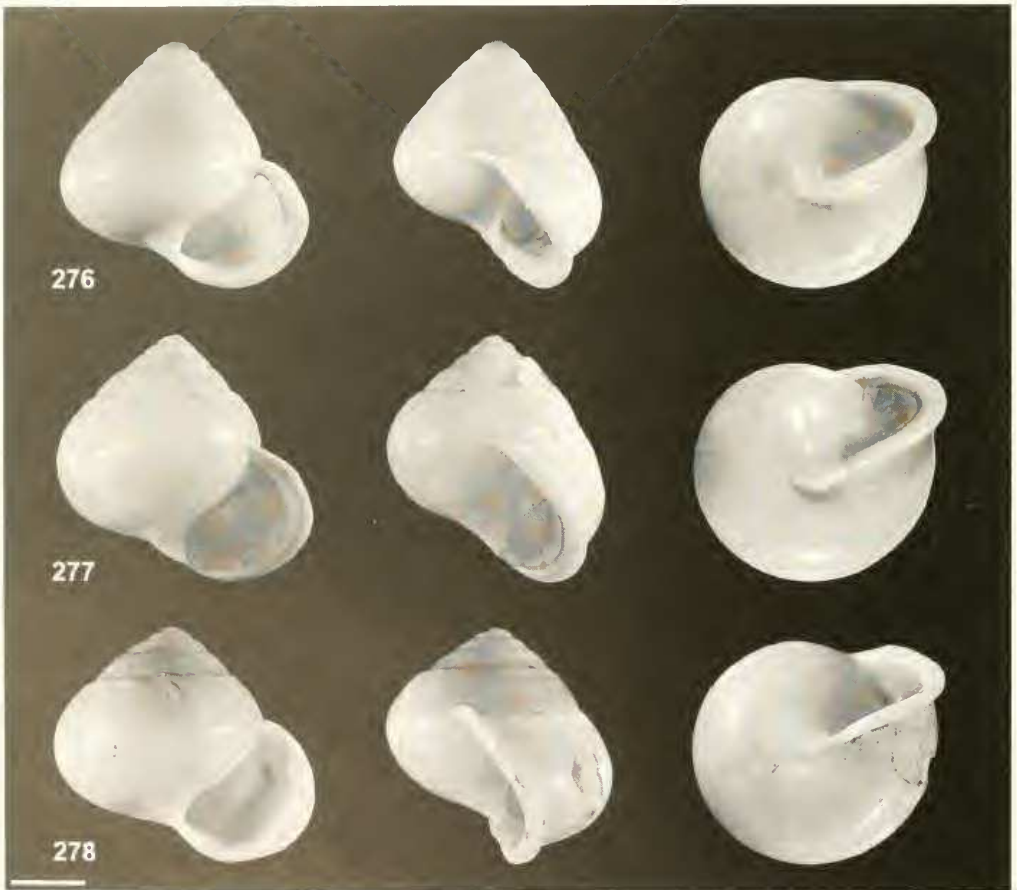
For comments, see under *Helicina tenuis*, *H. talamancensis*, *H. gemma*, and *H. monte-verdensis* n. sp.

Helicina oweniana coccinostoma
Morelet, 1849

Helicina oweniana var. *coccinostoma* – von Martens, 1900: 605–606: E-Costa Rica: Las Delicias, near Santa Clara, 400 m [10°57'37"N, 85°02'W, 40 m a.s.l., Alajuela Province] (Biolley) [*non* Morelet, 1849] refers most likely to *Helicina gemma*

Original Description

Helicina coccinostoma Morelet, 1849: 19 (not figured)



FIGS. 276–278. *Helicina* spp. FIG. 276. Syntype of *Helicina oweniana*, BMNH 20010751, height 8.3 mm; scale bar 2.5 mm. FIG. 277. Lectotype of *Helicina coccinostoma*, BMNH 1893.2.4.1605, height 8.3 mm; scale bar 2.5 mm. FIG. 278. Lectotype of *Helicina anozona*, ZMB 25604a, height 7.9 mm; scale bar 2.5 mm.

Type Material

BMNH 1893.2.4.1605–1608, Morelet coll., "Guatemala, Peten, Palenque"

The type lot contains four specimens from the Morelet collection, which was bought by H. Fulton and later purchased by the BMNH. To the shell of one specimen there was glued a small label "type". Because the origin of this label is uncertain and it is obviously not from Morelet himself the specimen is **herein chosen as lectotype**. The paralectotypes do not significantly differ from the lectotype, except for one specimen being less elevated.

The lectotype (Fig. 277) very closely resembles that of *Helicina anozona* in shape. Its color is lighter, yellowish opaque throughout, except for a whitish band directly under the suture and the yellowish outer lip.

Dimensions:

Lectotype BMNH 1893.2.4.1605

8.3/7.9/8.5/6.1/5.3/6.4/6.8 mm

Paralectotypes BMNH 1893.2.4.1606–1608

8.2/7.5/8.1/6.9/5.1/6.1/6.5 mm

7.6/7.8/8.3/6.9/5.1/5.9/5.9 mm

7.2/6.7/7.3/6.1/4.6/5.5/5.6 mm

Type Locality

"Petenensis sylvas" [Guatemala, Petén Department].

The status of the taxon is not further discussed here, because it lies beyond the scope of this study and requires the examination of more comprehensive Mexican and Guatemalan material.

Helicina oweniana anozona
von Martens, 1875

Helicina oweniana var. *anozona* – Biolley, 1897: 5: Costa Rica: Tuis, 600 m [about 09°51'N, 83°35'W, Cartago Province] and las Delicias (Santa Clara), 400 m [10°57'37"N, 85°02'W, 40 m a.s.l., Alajuela Province] [*non* von Martens, 1876] refers most likely to *Helicina gemma*

Helicina oweniana var. *anozona* – von Martens, 1900: 605–606: E-Costa Rica: Las Delicias, near Santa Clara, 400 m [10°57'37"N, 85°02'W, 40 m a.s.l., Alajuela Province] (Biolley), Tuis, 600 m [about 09°51'N, 83°35'W, Cartago Province]

(Pittier, Biolley) [*non* von Martens, 1876] refers most likely to *Helicina gemma*

Original Description

Helicina anozona von Martens, 1875: 649 (not figured); von Martens, 1876: 261, pl. 9, fig. 7

Type Material

Lectotype ZMB 25604a (leg. Salvin), 1 paralectotype ZMB 25604b (same data); 4 paralectotypes ZMB 40862 (same data) (present designation); syntypes (now paralectotypes) SNG 2192 (Zilch, 1979)

Von Martens based the description on specimens collected by Salvin housed in the collection of the ZMB, where he was curator at the time. One lot bears von Martens' sign for types, the larger specimen best matches the description and is **here selected as lectotype** (Fig. 278). The figure of *Helicina oweniana anozona* in von Martens (1890) is based on a specimen collected later by Champion (ZMB 103307).

The shell differs from *H. oweniana* in its general shape, a more globular appearance: the whorls are more strongly inflated, the spire is lower, the aperture relatively larger and the whorls are slightly shouldered. Except for the whitish color, the features of the outer lip are very similar.

Dimensions:

Lectotype: 7.9/8.4/8.9/7.5/5.4/6.3/6.3 mm

Type Locality

"Guatemala, vicinity of Coban" [Guatemala: Alta Verapaz].

The status of the taxon is not further discussed here, because it lies beyond the scope of this study and requires the examination of more comprehensive Mexican and Guatemalan material.

Helicina fragilis
Morelet, 1851

Alcadia (*Leialcadia*) *fragilis* – Wagner, 1908: 84–85: Costa Rica: Shirores, Talamanca [in part] [*non* Morelet, 1851] refers partially to *Helicina chiquitica*

See under *Helicina chiquitica* and *Helicina monteverdensis* n. sp.

MORPHOLOGICAL CHARACTERISTICS OF RELATED SUPRASPECIFIC TAXA OF AMERICAN HELICINIDAE

For the discussion of the arrangement of the Costa Rican species and the comparison of morphological characteristics, the following supraspecific taxa were investigated with emphasis on the less investigated features, for example, embryonic shell structure and the anatomy of the female reproductive system. When available, the respective type species were examined, otherwise species were chosen that are assumed to be closely related. The taxa encompass all important genera and subgenera, which include species reported for the Central American mainland and some selected representatives from South America and the Caribbean Islands. Unless otherwise stated, the synonymy given by Baker (1922a) is accepted and not repeated. A detailed listing of the objective synonyms can be found in Keen (1960). From the following taxa, *Helicina*, *Ceochasma*, *Alcadia*, *Lucidella*, *Eutrochatella*, *Pyrgodomus* and *Schasicheila* are commonly recognized at the generic level.

Because the following also gives an overview of these supraspecific taxa and their characteristics, *Succincta* and "*Cinctella*" were added only on the basis of annotated literature data. Furthermore, references for a few radula descriptions were given for completeness.

For the verification of the dissections, histological sections were studied for *Helicina jamaicensis*, *Alcadia hollandi*, *Lucidella aureola* and *Eutrochatella pulchella*. Similar attempts for *Helicina brasiliensis* and *Schasicheila alata* proved to be only partially successful due to the poor condition of the old material.

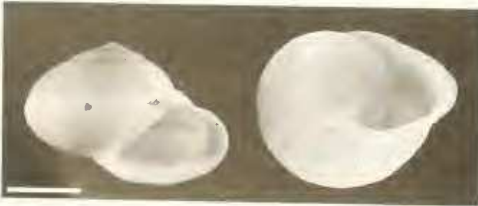


FIG. 279. *Helicina neritella*, IR 3454, height 9.8 mm; scale bar 5 mm.

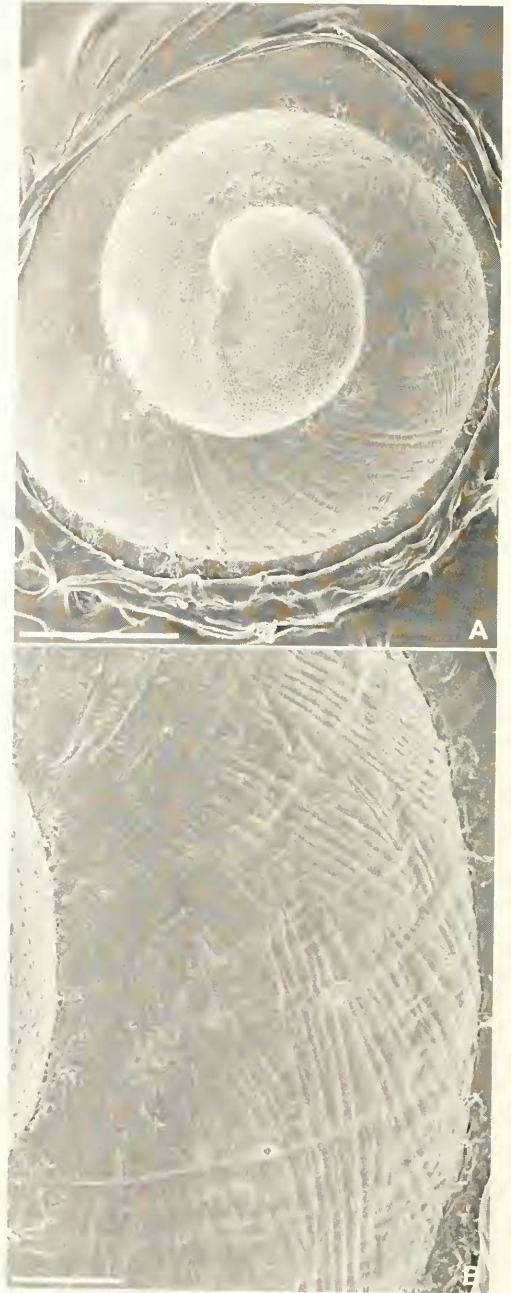


FIG. 280. Teleoconch surface structure of *Helicina neritella*, IR 3857. A. Structure of apical part. B. Pattern of oblique diverging grooves on the 1st whorl; scale bar 500 μ m (A), 100 μ m (B).

Helicina Lamarck, 1799

Type species

Helicina neritella Lamarck, 1799

Investigated Species

Helicina neritella (Figs. 279, 340A)

Material

Jamaica: Manchester Parish, Mandeville, Caledonia Road, 18°02'11"N, 77°30'44"W, 600 m a.s.l., 28./29.05.2001 (IR 3454, IR 3459); St. Ann Parish, N Ocho Rios, Fern Gully, 310 m a.s.l., 04.06.2001 (IR 3857), leg. W. Böckeler & I. Richling

Morphological Characteristics

Teleoconch Surface Structure (Fig. 280): The first half whorl is sculptured with the transitional pattern, which is followed by strongly developed oblique diverging grooves. This pattern is maintained throughout the teleoconch.

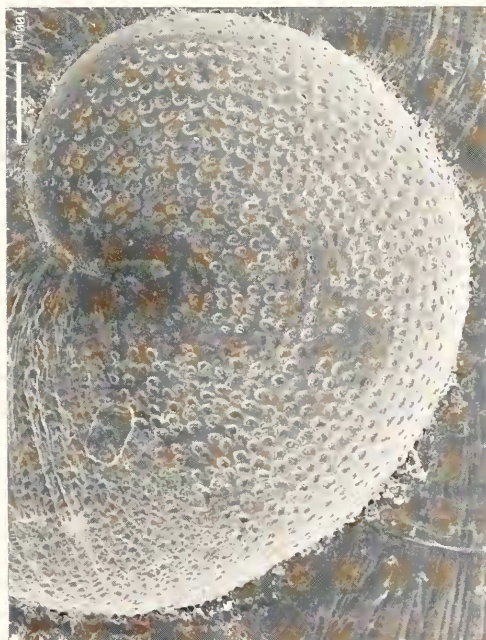


FIG. 281. Embryonic shell of *Helicina neritella*, IR 3459; scale bar 100 μ m.

Embryonic Shell (Fig. 281): Densely structured with pits arranged in concentric lines, pits comparatively large. Diameter about 728 μ m ($n = 3$), a little smaller than given by Thompson (1982), other structures equal to his description.

Radula: Figured in Baker (1922a: pl. III, fig. 6, pl. IV, fig. 17).

Female Reproductive System (Fig. 282): Ascending limb of the V-organ elongated, straight, in natural position overlapping with the posterior part of the pallial oviduct. The latter in relation to the apical complex remarkably long, transversally constricted. Small, oblong receptaculum seminis entering inner side of the descending limb. Bursa copulatrix very prominent and elongated with numerous, densely arranged, rather small lobules. Provaginal sac appearing vestigial, long and slender, only slightly demarcated from its much elongated and partially coiled stalk. Provaginal opening absent.



FIG. 282. Female reproductive system of *Helicina neritella*, apical complex enlarged, IR 3454; scale bars 2.5 mm (left), 1 mm (right).

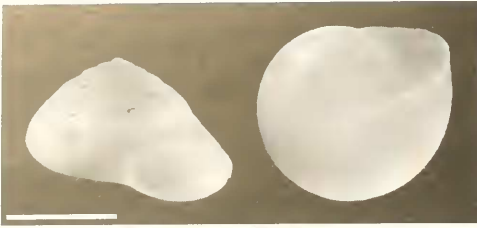


FIG. 283. *Helicina platychila*, UF 259486, height 6.5 mm; scale bar 5 mm.

Investigated Species

Helicina platychila (von Mühlfeldt, 1816) (Figs. 283, 340B)

Material

Dominica: along trail $\frac{1}{8}$ mi. W of Trafalgar Falls, upper end of banana plantation, leg. J. P. E. Morrison (JPEM-2610), 11.10.1965 (UF 259486)



FIG. 284. Embryonic shell of *Helicina platychila*, UF 259486; scale bar 100 μ m.

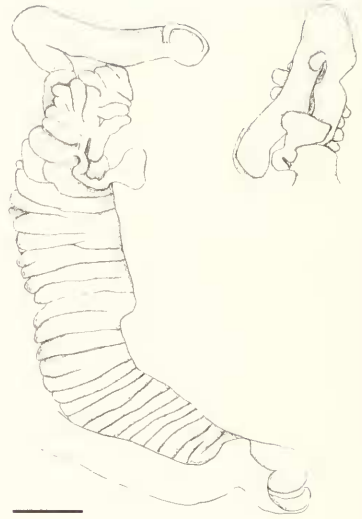


FIG. 285. Female reproductive system of *Helicina platychila*, right figure: dorsal view, UF 259486; scale bar 1 mm.

Morphological Characteristics

Embryonic Shell (Fig. 284): Similar pattern as in *Helicina neritella*, but pits smaller and more numerous. Diameter 890 μ m.

Female Reproductive System (Fig. 285): Very similar to that of *Helicina neritella*. Ascending limb of V-organ slightly curved; pallial oviduct relatively shorter and stronger folded. Bursa copulatrix prominent, with less numerous lobes, but the latter larger and elongated. Provaginal sac small, roundly triangular, stalk slightly curved and relatively long. Provaginal opening absent.

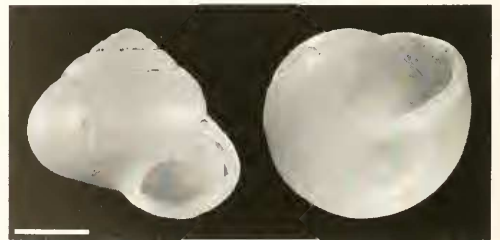


FIG. 286. *Helicina orbiculata*, IR 3361, height 6.5 mm; scale bar 2.5 mm.

Oligyra Say, 1818

Type species

Olygyra orbiculata Say, 1818

Investigated Species

Helicina orbiculata (Figs. 286, 340C)

Material

USA: Florida, Gainesville, Museum Road, near Dickinson Hall, 05.2001, leg. J. Slapcinsky & I. Richling (IR 3359, IR 3361)

Morphological Characteristics

Teleoconch Surface Structure (Fig. 287): Transitional pattern for about $1/3$ whorl, subsequently sculptured with oblique diverging grooves up to the aperture. Furthermore widely spaced, slightly impressed spiral grooves with periostracal ridges.

Embryonic Shell (Fig. 288): Scarcely sculptured with pits arranged in concentric lines. Interspaces of lines and pits exceed the size of the pits. Occasionally more densely pitted (Fig. 288B). Diameter 835 μm ($n = 4$).

Radula (Fig. 289): All centrals with cusps, A-central about 3–4, B-central about 5–6, C-central about 2–4; comb-lateral with 7–8 cusps. Cusps of the marginals rather slowly increasing in number, cusps more distally than laterally arranged. Except for minor deviations, this is in agreement with Baker (1922a).

Female Reproductive System (Fig. 290): V-organ rather stout, pallial oviduct moderately constricted. Receptaculum seminis large, bulbous, entering at inner side of descending limb of V-organ. Bursa copulatrix rather small and weakly lobed, of about the same size as elongated provaginal sac, which is slightly constricted at the distal side, its stalk is short. Provaginal opening absent. The female system was studied and figured by Baker (1926) (Fig. 9). Except for the monaulic (instead of diallic) conditions, the structures were confirmed. The bursa copulatrix differs in the length of its lobes in the specimens of all three locations (Baker: Miami County, Florida, and San Antonio,



FIG. 287. Teleoconch surface structure of *Helicina orbiculata*, IR 3859. A. Structure of apical part. B. Pattern of oblique diverging grooves and spiral grooves with periostracal ridges on the begin of the 2nd and 3rd whorl; scale bars 500 μm (A), 100 μm (B).



FIG. 288. Embryonic shell of *Helicina orbiculata*. A. IR 3359. B. IR 3361; scale bar 100 μ m.

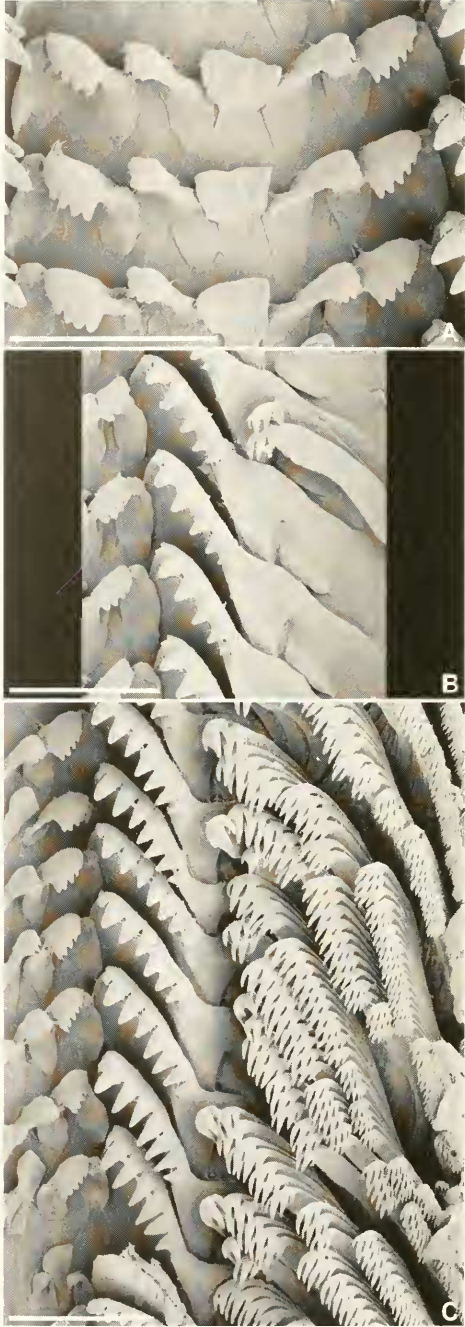


FIG. 289. Radula of *Helicina orbiculata*, IR 3359. A. Centrals. B. Comb-lateral. C. Marginals; scale bar 50 μ m.

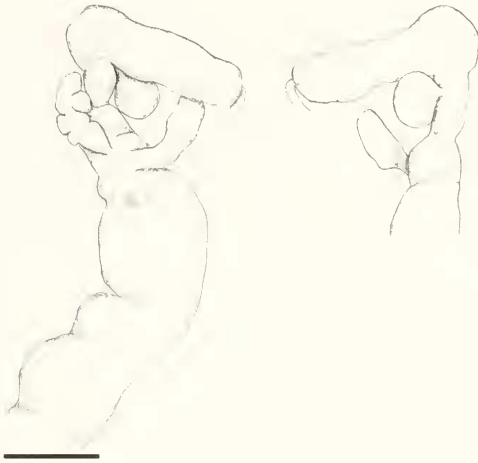


FIG. 290. Female reproductive system of *Helicina orbiculata*, IR 3361; scale bar 1 mm.

Texas), the presently studied specimens have furthermore a larger receptaculum seminis. Baker (1926) treated the specimens from Texas as the subspecies *Helicina orbiculata tropica* Jan, 1846, but a recent electrophoretic investigation by Strenth & Littleton (2000) suggests the conspecificity of both taxa, which has been discussed repeatedly.

Succincta Baker, 1922

Type species

Helicina succincta Martens, 1890

Investigated Species

Helicina succincta (investigated by Baker, 1928)

Morphological Characteristics

Radula: Figured in Baker (1928: pl. IV, fig. 26).

Female Reproductive System: Figured in Baker (1928: pl. II, figs. 3, 4): Receptaculum seminis remarkably enlarged and slightly trilobed; bursa copulatrix reduced in size and only bilobed; provaginal sac well developed and distally lobed, stalk quite long. According to the drawing and the results for re-examined mainland species, the provaginal opening is here assumed to be absent.



FIG. 291. *Helicina turbinata*, Cordova, ZMB 103315, height 11.7 mm; scale bar 5 mm.

Tristramia Crosse, 1863

Type species

Helicina salvini Tristram, 1861

Investigated Species

Helicina turbinata Wiegmann, 1831 (Figs. 291, 340D)

Material

Mexico: Arisolapa [?], leg. Strebel, #1723 (ZMH 2932)

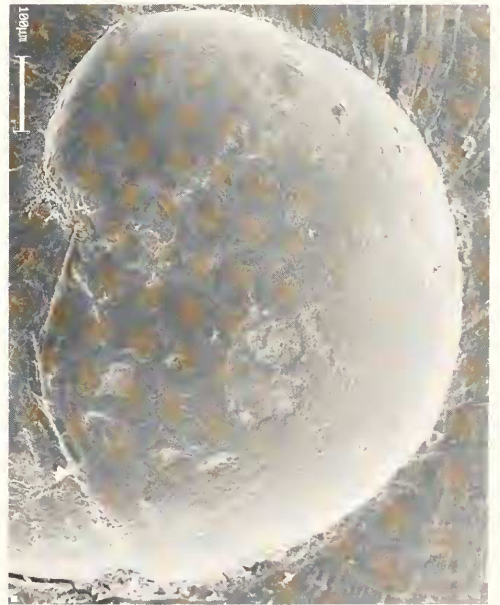


FIG. 292. Embryonic shell of *Helicina turbinata*, ZMH 2932; scale bar 100 μ m.

Morphological Characteristics

Embryonic Shell (Fig. 292): The surface is concentrically pitted, but due to the very small size of the widely spaced pits, the surface appears nearly smooth. Diameter 765 μm .

Radula: Figured in Baker for the closely related or synonymous species (von Martens, 1890–1901; Baker, 1922a) *Helicina zephyrina* Menke, 1830 (1922a: pl. III, fig. 9, pl. IV, fig. 13).

Female Reproductive System (Fig. 293): V-organ normally developed; pallial oviduct transversally and partially also longitudinally constricted. Receptaculum seminis very large and bulbous, entering at the inner side of the descending limb of the V-organ, but, due to its unusual size, shifted dorsally. Bursa copulatrix prominent and deeply lobed; provaginal sac with a rather slender stalk (not visible in Fig. 293), large and slightly constricted at its distal side. The provaginal opening is absent. Except for the erroneously assumed provaginal opening the description by Baker (1928) for *Helicina zephyrina* is identical, especially with re-



FIG. 293. Female reproductive system of *Helicina turbinata*, right figure: dorsal view, (on account of the poor preservation kept in nearly natural position) ZMH 2932; scale bar 1 mm.

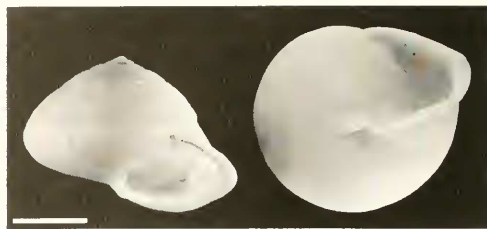


FIG. 294. *Helicina amoena*, ZMB 103345, height 10.6 mm; scale bar 5 mm.

spect to the shape of the bursa copulatrix and the enlarged receptaculum seminis.

Oxyrhombus Crosse & Fischer, 1893

Type species

Helicina amoena L. Pfeiffer, 1849

Investigated Species

Helicina amoena (Figs. 294, 340E)

Material

Guatemala: Teleman (ZMB 103345)

Morphological Characteristics

Embryonic Shell: The structure is similar to those shown for *Helicina funcki* and *H. pitalensis* (Figs. 15, 43): relatively large pits in concentric lines with their diameter about equal to their interspacial distance. Within the material available, large parts of the embryonic shell were so badly eroded so that it did not seem to be worth figuring. Diameter 860 μm .

Radula: Figured in Baker (1922a: pl. III, fig. 8, pl. IV, fig. 15).

Female Reproductive System (Fig. 295): In general similar to that of *Helicina turbinata*, but receptaculum seminis much smaller, bursa copulatrix with an elongated central axis from which numerous, further subdivided lobes branch off. Provaginal sac much more flattened and more strongly irregularly lobed at the distal side, its stalk of moderate length (not clearly visible in Fig. 295). Provaginal opening absent.

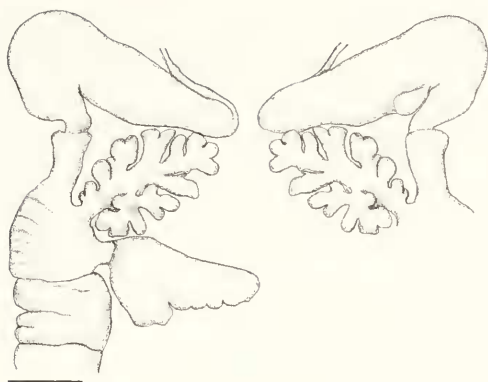


FIG. 295. Female reproductive system of *Helicina amoena*, right figure: dorsal view, distal parts omitted, ZMB 103345; scale bar 1 mm.

Pseudoligyra Baker, 1954

Synonym (objective)

Tenuis Baker, 1922, *non* Barrande, 1881

Type species

Helicina tenuis Pfeiffer, 1849

Investigated Species

Helicina tenuis – see above.

Punctisulcata Baker, 1922

Type species

Helicina punctisulcata von Martens, 1890

Investigated Species

Helicina punctisulcata cuericiensis n. subsp. – see above.

“*Cinctella*” Baker, 1922,
non Monterosato, 1884

Type species

Helicina cinctella Shuttleworth, 1852

Investigated Species

Helicina cinctella (investigated by Baker, 1928)

Morphological Characteristics

Female Reproductive System: Figured in Baker (1928: pl. II, fig. 5): Receptaculum of normal size; bursa copulatrix prominent and having several further subdivided lobes; provaginal sac weakly lobed at distal side, flattened. The provaginal opening is shown in the figure, but its existence is very questionable. Here it is assumed to be absent.

“*Gemma*” Baker, 1922,
non Deshayes, 1853

Type species

Helicina gemma Preston, 1903

Investigated Species

Helicina gemma – see above.

Tamsiana Baker, 1922

Type species

Helicina tamsiana Pfeiffer, 1851

Investigated Species

Helicina tamsiana

Material

Venezuela: Porto Cabello, leg. Martin (ZMB 103314)

Morphological Characteristics

Embryonic Shell: Only a single specimen was studied. It remains uncertain whether the embryonic shell is partially eroded or whether the surface is rather smooth, except for very scarce pits and very slight oblique lines.

Radula: Figured in Baker (1923: p. 20, fig. 20).

Female Reproductive System: Described and figured by Baker (1923: pl. VI, fig. 14): Receptaculum seminis of normal size; bursa copulatrix reduced to a very small, simple sac; provaginal sac very prominent and anteriorly elongated, so that the stalk branches off about the middle of its long side. Provaginal opening is shown in the figure, its existence remains questionable.



FIG. 296. *Helicina dysoni*, UF 226928, height 5.3 mm; scale bar 2.5 mm.

Analcadia Wagner, 1908

Type species

Helicina dysoni Pfeiffer, 1849

Investigated Species

Helicina dysoni (Figs. 296, 340F)

Material

Trinidad & Tobago: Trinidad Island, Mayaro County, Trinity District, 0.6 km SW junction



FIG. 297. Embryonic shell of *Helicina dysoni*, HNC 54607; scale bar 100 μ m.

Trinity Road & Guayaguayare Road (Rushville), 10°07'32"N, 61°03'28"W, 12 m a.s.l., leg. K. Auffenberg et al. (KA-1212), 02.06.1994 (UF 226928)

Venezuela: Margarita Island, Porlamar, just outside town under trees, ex Guido Poppe, 1988 (HNC 54607)

Morphological Characteristics

Embryonic Shell (Fig. 297): Surface with a few concentric rows of small, widely spaced pits. Diameter 590 μ m.

Radula: Figured by Baker (1923: pl. III, fig. 12).

Female Reproductive System (Fig. 298): Limbs of V-organ rather short, small receptaculum seminis entering at inner side of descending limb. Bursa copulatrix representing a very small sac, its connection to the reception chamber remarkably shifted towards the dorsal side compared to all other species described in this study. Provaginal sac exceptional large and inflated, slightly irregularly constricted at its distal side; stalk short, stout and branching off at the middle of the sac. Directly at junc-

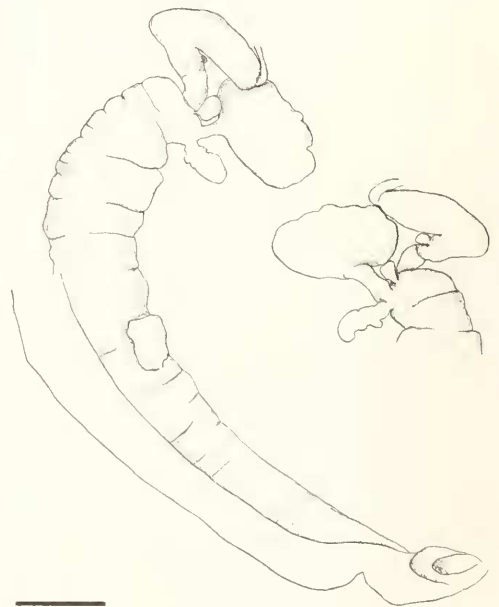


FIG. 298. Female reproductive system of *Helicina dysoni*, right figure: dorsal view, UF 226928; scale bar 1 mm.

tion with the reception chamber is an anterior sac-shaped appendage. Additional sac present at ventral side of the pallial oviduct which seems to be connected to it (remains to be checked histologically). Provaginal opening absent.

Sericea Wagner, 1907

Type species

Helicina sericea Drouet, 1859

Investigated Species

Helicina sericea (Figs. 299, 340G)

Material

Suriname: District Suriname, Bodensavanne [?], mine synagoge, leg. C.O. van Regteren Altena (loc. 51), 14.03.1963 (RMNH 8890)

Morphological Characteristics

Embryonic Shell (Fig. 300): Similar to that of *Helicina dysoni*. Diameter 755 μ m.

Female Reproductive System (Fig. 301): V-organ and receptaculum seminis similar to *Helicina dysoni*. Bursa copulatrix of moderate size and subdivided in numerous short lobules. Provaginal sac exceptional large and inflated, nearly kidney-shaped, with its short and stout stalk branching off at about the middle of the proximal side. It bears an anterior basal appendage at the junction with its stalk, which is roundly constricted twice. Provaginal opening absent.



FIG. 299. *Helicina sericea*, RMNH 8890, height 5.1mm; scale bar 2.5 mm.



FIG. 300. Embryonic shell of *Helicina sericea*, RMNH 8890; scale bar 100 μ m.



FIG. 301. Female reproductive system of *Helicina sericea*; upper, right figure: dorsal view, RMNH 8890; scale bar 1 mm.

Ceochasma Thompson, 1968

Type species

Ceochasma phrixina Thompson, 1968

Investigated Species

Ceochasma phrixina

Material

Mexico: Colima, 0.3 km. SE Tamala, 152 m a.s.l., leg. F.G. Thompson (FGT-777), 02.08.1966 (UF 20139, Paratypes)

Morphological Characteristics

Embryonic Shell: Not examined.

Radula: Figured in Thompson (1968: 49).

Female Reproductive System: Described and figured by Thompson (1968: 49), for this study only reinvestigated with respect to provaginal opening, which was found to be absent.

Angulata Baker, 1922

Type species

Helicina angulata Sowerby, 1842

Investigated Species

Helicina brasiliensis Gray, 1825 (Figs. 302, 340H)

Material

Brazil: Sta. Catharina, Humboldt District, Joinville, Flussgebiet von Itaporu [area of



FIG. 302. *Helicina brasiliensis*, ZMH 2931, height 5.6 mm; scale bar 2.5 mm.

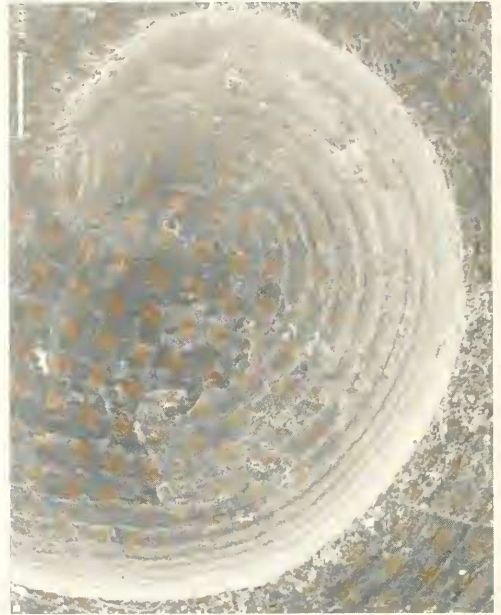


FIG. 303. Embryonic shell of *Helicina brasiliensis*, ZMH 2931; scale bar 100 μ m.

the Rio Iguaçu], leg. W. Ehrhardt, purchased 21.10.1910 (ZMH 2931)

Morphological Characteristics

Embryonic Shell (Fig. 303): Sculptured with regular, broad, very slightly raised spiral bands; interspacial distance smaller than the width of these bands, otherwise smooth. Diameter 695 μ m ($n = 2$).

Female Reproductive System (Fig. 304): Receptaculum seminis very small, connected to the inner side of the descending limb of the V-organ; bursa copulatrix large and deeply lobed. Provaginal sac elongated and of somewhat irregular outline, its stalk rather stout. Provaginal duct seems to branch off from this stalk at its most anterior point. Due to the poor preservation of the material, the provaginal duct and opening could not be observed with certainty, but its presence is very likely.

Alcadia Gray, 1840

Type species

Helicina major Gray, 1824

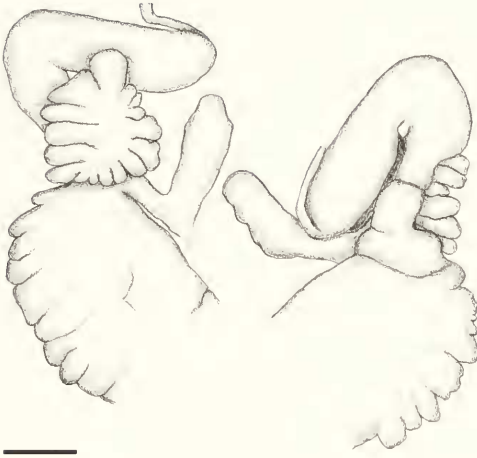


FIG. 304. Female reproductive system of *Helicina brasiliensis*, right figure: dorsal view, (distal parts omitted, provaginal duct and opening likely, but not verified) ZMH 2931; scale bar 0.5 mm.

Investigated Species

Alcadia major (Figs. 305, 340I)

Material

Jamaica: Manchester Parish, Silver Grove, Secondary forest & bordering pasture, limestone & red soil, 18°04.95'N, 77°35.35'W, 880–900 m a.s.l., leg. G. Rosenberg & I.V. Muratov (JBS 113), 02.10.1999 (ANSP 19559)

Morphological Characteristics

Embryonic Shell (Fig. 306): Surface with more or less strong oblique grooves, more pronounced towards the margin, and coarse,

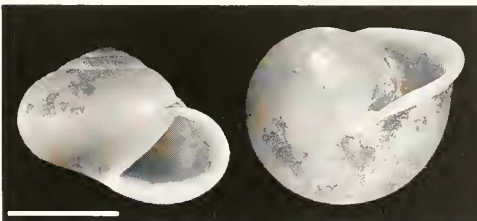


FIG. 305. *Alcadia major*, ANSP 19559, height 14.2 mm; scale bar 10 mm.

irregularly spaced radial threads. Diameter 1800 μ m. The embryonic shell had also been studied and figured by Thompson (1982: fig. 26), his specimen shows the oblique grooves within the inner curvature, the diameter is given with 1.0 mm, but a measurement of the figure reveals a more likely size of about 2.2 mm.

Radula (Fig. 307): The centrals completely lack cusps and the cutting edges are reinforced. The "comb"-lateral agrees in its rough outline rather with the denticulated part of the comb-lateral in *Helicina*, but the cutting edge is smooth and thickened and resembles the T-shaped lateral of *Eutrochatella* (vianid radula). The accessory plate seems to be reduced. The tips of the marginals are rounded and show minor crenulations.

The vianid condition of the radula has already been mentioned by Boss & Jacobson (1973) and Thompson (1982), but it has never been figured and described in detail before.

Female Reproductive System (Fig. 308): V-organ with a slight apical swelling, its as-



FIG. 306. Embryonic shell of *Alcadia major*, ANSP 19559; scale bar 100 μ m.

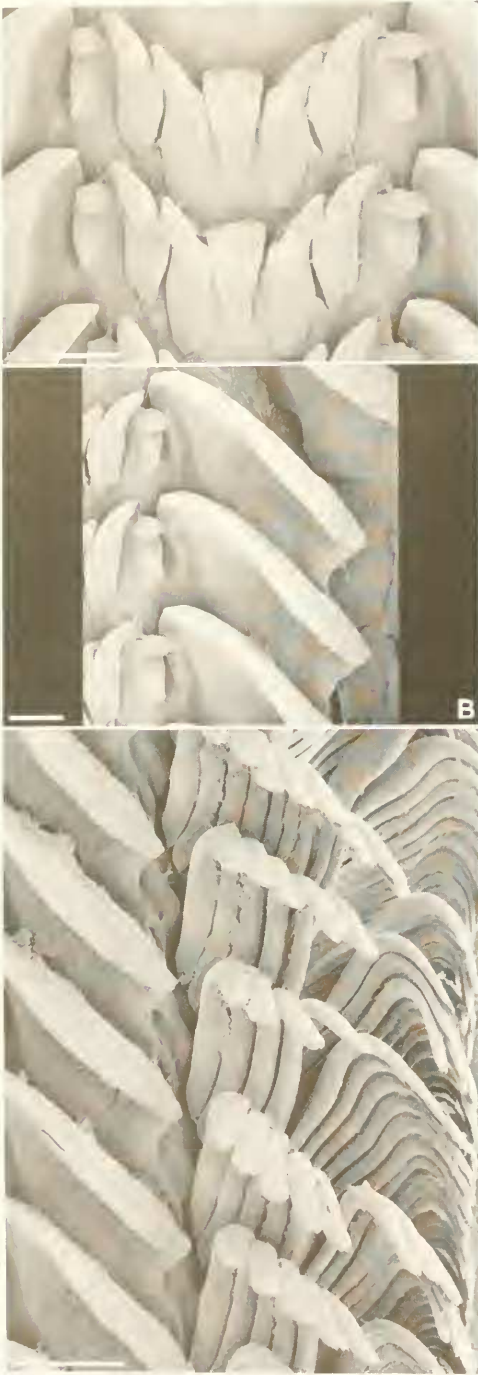


FIG. 307. Radula of *Alcadia major*, IR 3359. A. Centrals. B. Comb-lateral. C. Marginals; scale bars 50 μ m (A, B), 100 μ m (C).



FIG. 308. Female reproductive system of *Alcadia major*, ANSP 19559; scale bar 2.5 mm.

ending limb slightly elongated. Receptaculum seminis equal to *Helicina* on the inner side of the descending limb, pedicel well developed. Bursa copulatrix representing a very large, irregularly shaped sac that broadly enters the reception chamber. Close to this connection is a slender provaginal duct that extends up to its opening for about $\frac{1}{3}$ of the length of the pallial oviduct. Close to the reception chamber, the provaginal duct receives the stalk of the medium-sized, oblong provaginal sac. The specimen is not very well preserved and perhaps the visible broad connection of the bursa copulatrix does not reflect the natural condition nor does the weakly demarcated distal end of the reception chamber.



FIG. 309. *Alcadia hollandi*, IR 3579, height 7.4 mm; scale bar 5 mm.

Palliata Baker, 1922

Type species

Helicina palliata C. B. Adams, 1849

Investigated Species

Alcadia hollandi (C. B. Adams, 1849) (Figs. 309, 340J)

Material

Jamaica: Manchester Parish, Mandeville, 600 m a.s.l., Marshall's Drive, 25./27.05.2001, leg. W. Böckeler & I. Richling (IR 3579)

Morphological Characteristics

Embryonic Shell (Fig. 310): Inner curvature with predominant irregular axial threads, towards the margin interposing with strong, very distinct oblique grooves. Diameter 840 μ m ($n = 2$).

Radula: Figured in Bourne (1911: pl. XL, fig. 56). Similar to *Helicina*: with denticulated

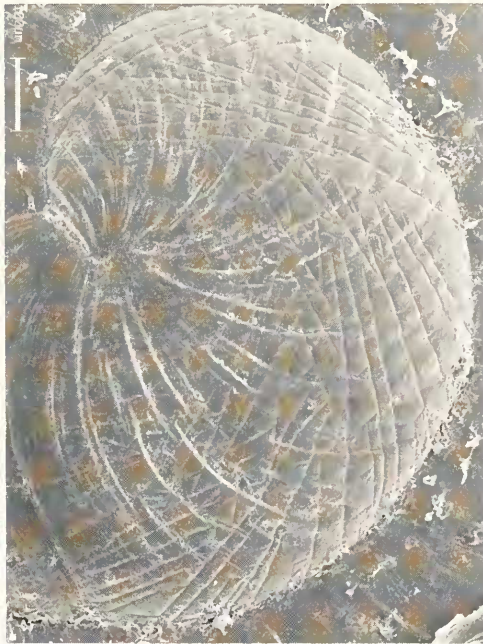


FIG. 310. Embryonic shell of *Alcadia hollandi*, IR 3579; scale bar 100 μ m.

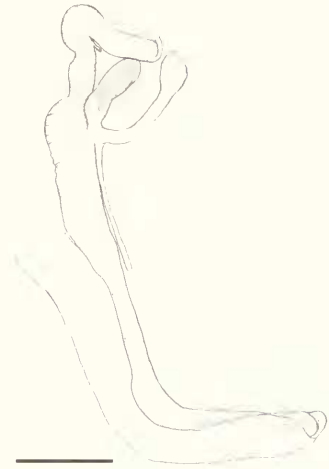


FIG. 311. Female reproductive system of *Alcadia hollandi*, IR 3579; scale bar 1 mm.

centrals and marginals, comb-lateral with cusps and accessory plate.

Female Reproductive System (Fig. 311): Ascending limb of V-organ shorter than in *Alcadia major*; receptaculum seminis small, located on the inner side of descending limb.

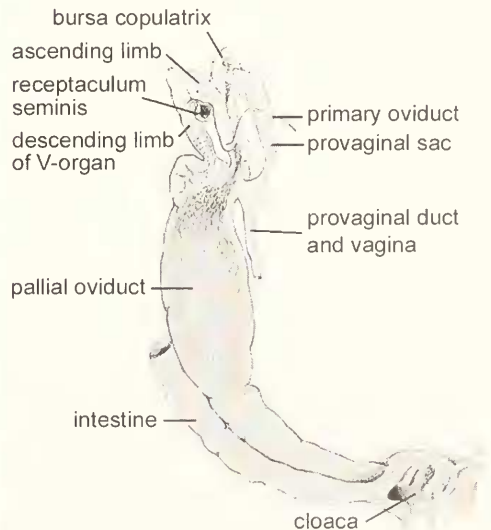


FIG. 312. Female reproductive system of *Alcadia hollandi* (reproduced from Bourne, 1911, explanations modified).



FIG. 313. *Alcadia jamaicensis*, IR 3502, height 8.3 mm; scale bar 5 mm.

Bursa copulatrix representing an oblong sac, longitudinally folded inside. Provaginal sac rather small and at the end of the very long stout stalk or itself stalk-like elongated, entering the reception chamber at nearly the same point as the bursa copulatrix and the provaginal duct. The latter is long and slender and opens at about $\frac{1}{3}$ of the way from the beginning of the pallial oviduct. The female system was figured by Bourne (1911: pl. XXXV, fig. 25, reproduced here: Fig. 312), but Baker (1926) questioned its correctness. Bourne's description is verified by

the present investigation, only that sperm had not been found within the pallial oviduct, probably due to different physiological conditions.

Investigated Species

Helicina jamaicensis Sowerby, 1841 (Figs. 313, 340K) (belongs to *Alcadia*, an assignment to a subgenus, e.g., *Palliata*, is here not intended)

Material

Jamaica: Manchester Parish, W Bellefield, valley near road to Banana Ground, 18°04'46" N, 77°26'27"W, 580 m a.s.l., 24.05.2001 (IR 3502); Manchester Parish, Mandeville, 600 m a.s.l., Marshall's Drive, 25./27.05.2001 (IR 3574), leg. W. Böckeler & I. Richling

Morphological Characteristics

Embryonic Shell (Fig. 314): Very similar to *Alcadia hollandi*. Diameter 920 μ m.



FIG. 314. Embryonic shell of *Alcadia jamaicensis*, IR 3574; scale bar 100 μ m.



FIG. 315. Female reproductive system of *Alcadia jamaicensis*, left figure: natural position, right figure: slightly lateral view, IR 3502; scale bar 1 mm.

Female Reproductive System (Fig. 315): V-organ similar to *Alcadia hollandi*; receptaculum seminis larger. Bursa copulatrix, provaginal sac and provaginal duct very closely associated. Bursa copulatrix more prominent than in *Alcadia hollandi*, its position is similar. Provaginal sac of nearly the same size as the bursa copulatrix, forming an elongated sac with a short, stout stalk, which rather connects with the provaginal duct than with the reception chamber. Provaginal duct slightly inflated shortly before its opening at about $\frac{2}{5}$ of the way from the beginning of the pallial oviduct. The latter only with minor constrictions.

Idesa H. Adams & A. Adams, 1856

Synonym (objective)

Leialcadia Wagner, 1907

Type species

Helicina rotunda Orbigny, 1841

Investigated Species

Alcadia rotunda (Figs. 316, 340L)

Material

Cuba: Pinar del Rio, Rangel, leg. M.L. Jaime (ZMB 90412)

Morphological Characteristics

Embryonic Shell (Fig. 317): Sculptured with fine, oblique diverging grooves. Diameter 690 μ m.

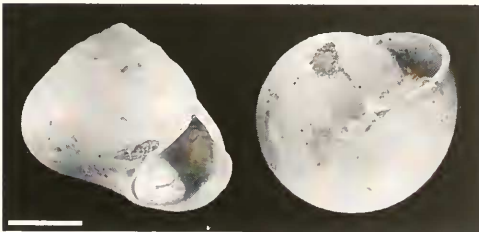


FIG. 316. *Alcadia rotunda*, ZMB 90412; scale bar 2.5 mm.



FIG. 317. Embryonic shell of *Alcadia rotunda*, ZMB 90412; scale bar 100 μ m.

Radula: Figured by Troschel (1856–1863: pl. V, figs. 10, 11) and Baker (1923: pl. III, fig. 13). Centrals and marginals with cusps, comb-lateral denticulated and with accessory plate.

Female Reproductive System: unknown.

***Microalcadia* Richling, n. subgen.**

Type species

Helicina hojarasca Richling, 2001

Investigated Species

Alcadia hojarasca – see above.

***Eutrochatella* Fischer, 1885**

Type species

Helicina pulchella Gray, 1825

Investigated Species

Eutrochatella pulchella (Figs. 318, 340M)

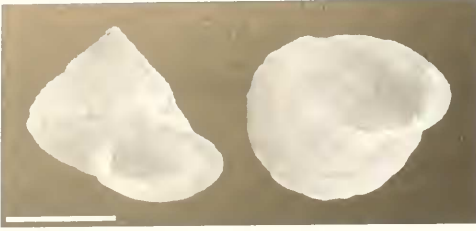


FIG. 318. *Eutrochatella pulchella*, IR 3702, height 7.9 mm; scale bar 5 mm.

Material

Jamaica: Manchester Parish, W Bellefield, valley near road to Banana Ground, 18°04'46" N, 77°26'27"W, 580 m a.s.l., 24.05.2001 (IR 3504); Trelawny Parish, near Burnt Hill, along road to Clarks Town, 18°18'24" N, 77°33'46"W, 510 m a.s.l., 02.06.2001 (IR 3808), leg. W. Böckeler & I. Richling

Morphological Characteristics

Embryonic Shell (Fig. 319): Surface rough, somewhat irregularly wrinkled. These

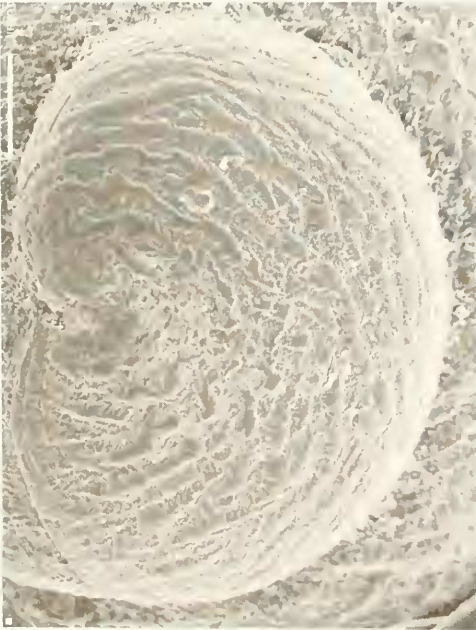


FIG. 319. Embryonic shell of *Eutrochatella pulchella*, IR 3505; scale bar 100 μ m.

coarse ridges and grooves show an orientation similar to the grooves in *Alcadia*. Diameter 560 μ m ($n = 3$).

Radula: Figured in Bourne (1911: pl. XL, fig. 57) and Baker (1922a: pl. VI, figs. 31–32). All teeth without cusps, except for the outermost marginals, lateral reinforced and T-shaped, accessory plate reduced.

Female Reproductive System (Fig. 320): V-organ of moderate size; receptaculum seminis small and located at the inner side of the descending limb. Bursa copulatrix large, oblong, externally not further subdivided, broadly connected with the reception chamber. Provaginal sac smaller than bursa copulatrix and flattened, lobed at the distal side, its stalk short and slender. The transition of the reception chamber to the pallial oviduct is externally only weakly visible; furthermore, the pallial oviduct of different investigated specimens was remarkably less thickened than in the species of *Helicina* for example, although the specimens were all mature. The provaginal opening is absent. Bourne (1911: pl. XXXV, fig. 26) did not recognize the monaulic condition; furthermore, his figure shows a larger bursa copulatrix.

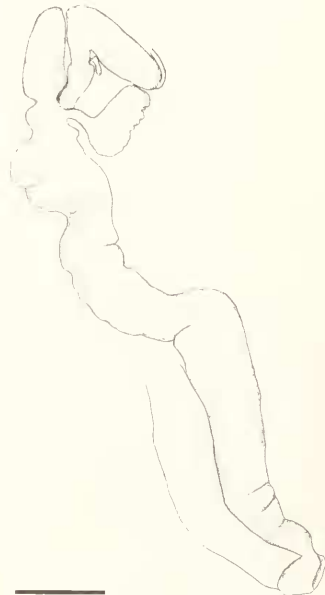


FIG. 320. Female reproductive system of *Eutrochatella pulchella*, IR 3808; scale bar 1 mm.



FIG. 321. *Lucidella aureola*, IR 3852, height 5.1mm; scale bar 2.5 mm.

Pyrgodomus Crosse & Fischer, 1893

Type species

Helicina chryseis Tristram, 1861

Investigated Species

Pyrgodomus microdinus – see above.

Lucidella Swainson, 1840

Type species

Helix aureola Férussac, 1822

Investigated Species

Lucidella aureola (Figs. 321, 340N)

Material

Jamaica: Manchester Parish, Mandeville, 600 m a.s.l., Marshall's Drive, 25./27.05.2001 (IR 3578); St. Ann Parish: N Ocho Rios, Fern Gully, 310 m a.s.l., 04.06.2001 (IR 3852), leg. W. Böckeler & I. Richling

Morphological Characteristics

Internal Shell Structures: (Fig. 322)

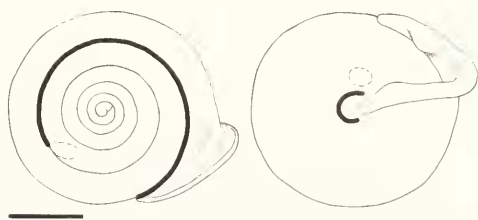


FIG. 322. Axial cleft and muscle attachments of *Lucidella aureola*, IR 3578; scale bar 2.5 mm.

Embryonic Shell (Fig. 323): Sculptured with numerous small pits, which are less regularly arranged than in *Helicina*. Their diameter is smaller than the interspacial distance. Diameter: 515 μm ($n = 3$). This is in full agreement with the description by Thompson (1982: figs. 24, 25).

Radula: Figured and described by Bourne (1911: pl. XL, fig. 59), Baker (1922a: pl. III, fig. 4, pl. V, fig. 22), and Thompson (1982: figs. 14, 15).

Female Reproductive System (Fig. 324): V-organ with a left-sided apical swelling, limbs rather short. Receptaculum seminis absent. Bursa copulatrix small, simple, broadly connected with the reception chamber. Provaginal sac large, distal side remarkably lobed, stalk branching off at about the middle, short and stout. Provaginal duct short, joining reception chamber nearly together with the stalk of the provaginal sac and the bursa copulatrix, opening at about distal end of the reception chamber. Posterior part (about $\frac{1}{4}$ to $\frac{1}{5}$) of pallial oviduct largely inflated and with numerous internal, longitudinal folds, at the distal end of this



FIG. 323. Embryonic shell of *Lucidella aureola*, IR 3852; scale bar 100 μm .



FIG. 324. Female reproductive system of *Lucidella aureola*, IR 3852; scale bar 0.5 mm.

structure enters an additional, long sac. In both structures, sperm were found. Baker's (1926: pl. VII. fig. 19) description based on badly macerated specimens has to be corrected with respect to the absence of the receptaculum seminis and the additional structures of the pallial oviduct.

Perenna Guppy, 1867

Type species

Helicina lamellosa Guppy, 1867

Investigated Species

Lucidella lirata – see above.



FIG. 325. *Schasicheila alata*, UF 251373, height 8.4 mm; scale bar 5 mm.

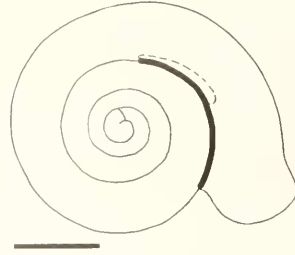


FIG. 326. Axial cleft and right muscle attachment of *Schasicheila alata*, ZMH 2928; scale bar 2.5 mm.

Schasicheila Shuttleworth, 1852

Type species

Helicina alata Pfeiffer, 1848

Investigated Species

Schasicheila alata (Figs. 325, 3400)

Material

Mexico: Agua Caliente, leg. Strebel (#1725) (ZMH 2928); Veracruz, 2.7 mi S Orizaba, 3,800 feet, leg. M.L. Paulson et al., 12.08.1965 (UF 251373)

Morphological Characteristics

Internal Shell Structures: (Fig. 326)

Embryonic Shell (Fig. 327): Sculptured with very regular and prominently raised axial folds. Diameter 1015 μ m.

Radula: Figured in Baker (1928: pl. V, fig. 27).

Female Reproductive System (Fig. 328): Both limbs of the V-organ remarkably elongated and curved, a receptaculum seminis developed as in *Helicina*, *Alcadia* and *Eutrochatella* is absent, but in all dissected specimens an accumulation of sperm was found within the oviduct proximal to the weekly separated pedicel. A bursa copulatrix similar to other genera is not present; instead, a large, strongly recurved sac, which seems to be fused with the pedicel extends dorsal to the V-organ, is present. The provaginal sac is rather small and flattened, slightly lobed at the distal side; its stalk is very short. Provaginal duct also very short, opening at



FIG. 327. Embryonic shell of *Schasicheila alata*, ZMH 2928; scale bar 100 μ m.

about the beginning of the pallial oviduct. The investigation confirms the description given by Baker (1928: pl. IV, figs. 19, 20).



FIG. 328. Female reproductive system of *Schasicheila alata*, V-organ turned to the left, UF 251373; scale bar 1 mm.

DISCUSSION

Knowledge of Costa Rican Helicinidae

Previous to this study and Richling (2001), six correctly identified species and one correctly identified subspecies (*Helicina funcki*, *H. pitalensis*, *H. tenuis*, *H. beatrix beatrix*, *H. beatrix confusa*, *H. gemma*, *Lucidella lirata*) of Helicinidae were known in Costa Rica. Additionally, a species of "*Pyrgodomus*" had tentatively been listed. The present investigation adds seven new species (*H. escondida* n. sp., *H. echandiensis* n. sp., *H. talamancensis*, *H. monteverdensis* n. sp., *H. chiquitica*, *Alcadia hojarasca*, *A. boeckeleri*) and two new subspecies (*Helicina punctisulcata cuericiensis* n. subsp., *H. beatrix riopejensis* n. subsp.). In addition, previously separated subspecies of *Helicina funcki* and *H. tenuis* were shown to have fallen within the range of intraspecific variability. The new and verified record of *Helicina flavida* remains doubtful in its interpretation. Furthermore, the re-examination of original material and records or their critical consideration demonstrated the absence of the Mexican and Guatemalan species *Helicina amoena*, *H. oweniana* and subspecies and *H. fragilis* from the Costa Rican fauna.

On one hand, the remarkable number of new species reflects the vague knowledge about the discrimination of the described taxa subsequent to the well founded major contributions at the end of the 19th century (e.g., von Martens, 1890–1901; Fischer & Crosse, 1880–1902), that is, the necessity of the examination of the type material. On the other hand, the recent discovery of strikingly different species (e.g., *Helicina echandiensis* n. sp.) in remote areas or the small species *Alcadia hojarasca* and *A. boeckeleri* dwelling in leaf litter illustrates the deficits in the inventory of the fauna, as well the difficulties in finding specimens at all, be it due to the very low abundance or to locally restricted ranges.

Distribution of Costa Rican Species and Faunal Composition

The knowledge of the distribution is limited by the insufficient investigation of the molluscan fauna of the adjacent areas Nicaragua and Panama. Despite considerable collecting efforts, information remains fragmentary for several species within Costa Rica itself. Nevertheless, some general aspects emerge. In the following, "southern Central America" will

refer to the area from the Nicaraguan depression to about the Canal Zone.

The Costa Rican helicinid fauna is composed of the following elements:

- (1) widespread species: *Helicina tenuis*, *Lucidella lirata*, *Pyrgodomus microdinus*
 - (2) species limited to southern Central America: *Helicina funcki*, *H. pitalensis*, *H. beatrix*, *H. tamancensis*, *H. gemma*, *H. monteverdensis* n. sp., *H. escondida* n. sp., *H. chiquitica*
 - (3) species occurring very locally: *Helicina punctisulcata cuericiensis* n. subsp., *H. echandiensis* n. sp., *Alcadia hojarasca**, *A. boeckeleri***
- * distributional pattern assumed for the taxon because affinities doubtful
 - ** distribution too poorly known to be discussed further.

The list shows that most species are endemic to southern Central America. This fact greatly changes the previous idea about the faunal composition with more widely spread and less endemic species due to the exclusion of three misidentified Mexican/Guatemalan species and the recognition of several new taxa.

Considering the distribution of these groups within Costa Rica, it becomes obvious that only the widely spread species occur on the Pacific as well as on the Caribbean side. *Pyrgodomus microdinus* represents an exception, because its distribution is mainly influenced by its strict limitation to calcareous outcrops. The other species can be further subdivided by their restriction to the:

Caribbean side: *Helicina funcki*, *H. beatrix*, *H. gemma*, *H. chiquitica*, *H. monteverdensis* n. sp., *H. escondida* n. sp.

Pacific side: *Helicina pitalensis*, *H. tamancensis*.

Mountain region: *Helicina echandiensis* n. sp., *H. punctisulcata cuericiensis* n. subsp.

Only the Caribbean species normally cross the continental divide in the Cordillera de Tilarán (e.g., Monteverde) and the Cordillera de Guanacaste, disappearing towards the Pacific plains. The Pacific species are restricted to the southern area and to the northern foothills of the Cordillera de Talamasca. The Peninsula de Nicoya and the central and northern plains and foothills of the Pacific side are virtually uninhabited by any species of the

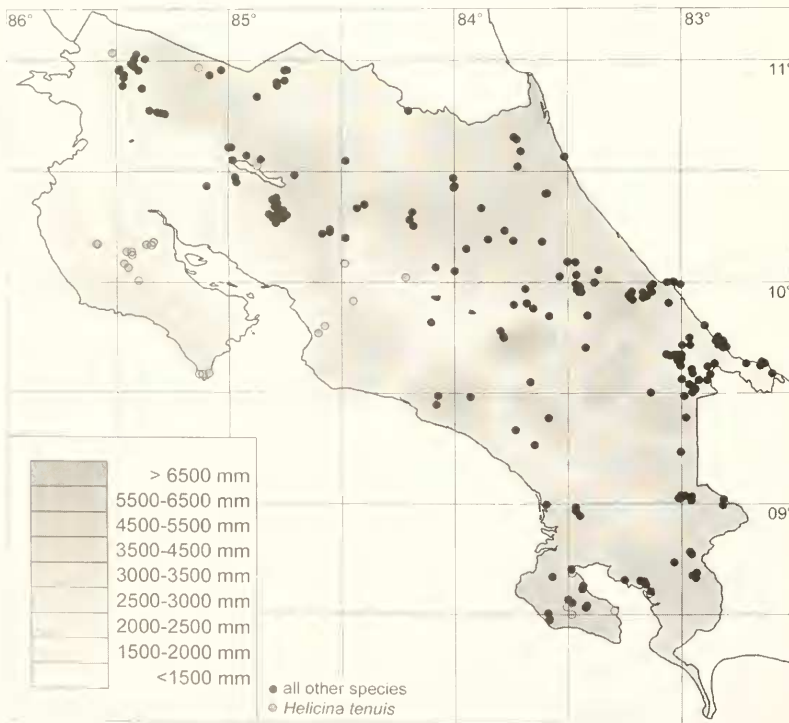


FIG. 329. Costa Rican records of Helicinidae mapped on the annual precipitation [mm/year], *Helicina tenuis* individually marked.

Helicinidae, except for *Helicina tenuis*. This is clearly related to the drier climate.

In conclusion, it can be stated that whereas in southern Costa Rica the continuously highly elevated mountain chain of the Cordillera de Talamanca obviously represents a barrier for the distribution of species; it is replaced more to the north by a dry belt along the northern plains and foothills up to the Valle Central.

The maps (Figs. 329, 330) show the locations of all records of Helicinidae in Costa Rica (*Helicina tenuis* differently marked) mapped on the distribution of the vegetation or the annual precipitation respectively (Ministerio de Agricultura y Ganaderia & Instituto Meteorológico Nacional, 1985). The meteorological data reflect the amount of annual rain and also provide a rough estimation of the real humidity available for the fauna, but do not reflect the strong seasonal changes during the dry period in the northwestern and central parts of the country. These conditions are much better represented by the vegetation, here given in a simplified map (modified after Tosi, 1969), graduated solely according to the humidity-related type of vegetation. As may be expected, the vegetation

map actually matches the distribution of the snails in the northwestern part much better. The single dot in the dry forest area (or < 1,500 mm/year rain-area) belongs to an old, subsequently localized record of *Helicina funcki* ("10 mi W of Tilarán"). If it is really correctly plotted, the specimen may also have come from a more humid river valley. On the Caribbean side which lacks such contrasting seasonal changes, a similar correlation cannot be found and the distribution of Helicinidae is probably not limited by climatic conditions.

Morphological Characteristics

In the following section the different characteristics will be discussed under general aspects, their applicability for species differentiation, i. e. mainly for the Costa Rican species, and their value for higher systematics within the Helicinidae.

Teleoconch Shape

The shape and color of the teleoconch are assumed to be directly affected by environ-

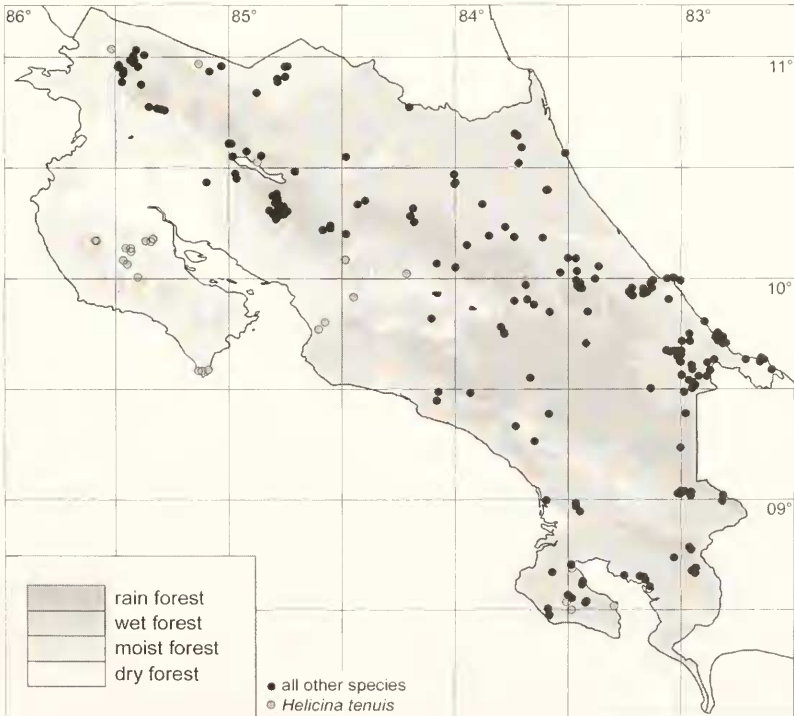


FIG. 330. Costa Rican records of Helicinidae mapped on the types of vegetation, *Helicina tenuis* individually marked.

mental selective pressures and therefore highly adaptable. On one hand, differences may therefore characterize different species, but on the other hand, under different environmental conditions a high plasticity may occur within a single species as well. Likewise, there is a high probability of convergent developments reducing the applicability of these features in higher systematic.

Aspects of the shell color will be discussed separately, along with the soft body color. Due to their practical importance at the species level, also for the determinations, shell characteristics were already discussed in the species accounts. In the following only certain general aspects will be considered.

Despite the outline of the shell, the development of the aperture is an important feature for the differentiation of the Costa Rican species. The aperture is always more or less oblique, but may be straight or curved backwards in its middle portion. The outer lip is flatly expanded or reflexed. The main function of the outer lip of the aperture is obviously the tight attachment to leaves or other surfaces of an aestivating individual. This is especially important for all arboreal species, such as the Costa Rican representatives of *Helicina*. Two different trends are realized to achieve an optimal attachment: (1) the basal part of the outer lip near the transition to the columella is protruded, thus forming a denticle, and is combined with a rather straight aperture (e.g., *Helicina tenuis*), or (2) the basal part is straight or even forms a little notch, but the middle portion of the aperture is strongly curved backwards (e.g., *Helicina beatrix*). Especially the slight basal notch present in all Costa Rican species that Wagner (1907–1911) summarized under the species group “*Gemma*” was used as indication for the inclusion in the subgenus *Leialcadia*. This classification turned out to be wrong, and the similarities can be explained by convergent developments in adaptation to the arboreal life, as is the feature of colorful shells included in the description of the *Leialcadia*. Another striking example for the misleading shell characteristics is illustrated by *Alcadia jamaicensis* (actual arrangement, based on features of embryonic shell and female reproductive system) which has formerly been classified as *Helicina jamaicensis* (e.g., Wagner, 1907–1911).

By the inclusion of *Analcadia* and *Sericea* into *Helicina*, the presence of periostracal hairs

adds another example of convergence and shows the unreliability of shell characteristics as an indicator for relationships. Within the family of Helicidae periostracal hairs are known to occur within at least in four different genera, *Helicina*, *Alcadia*, *Lucidella* (*L. adamsiana* L. Pfeiffer, 1849) and *Schasicheila*, the distinctness of which is strongly supported by characteristics of the female reproductive system and embryonic shell structures. The periostracal hairs seem to be related to a life within the leaf litter, they are also developed in other families of land snails (e.g., Helicidae).

Teleoconch Surface Structure

Among the Costa Rican representatives of the genus *Helicina*, two different traits in teleoconch surface structure can be recognized, a rough surface with oblique diverging grooves or a very smooth shell. Only one species (*Helicina escondida* n. sp.) shows an intermediate characteristic with the former structure only very weakly developed. Because in all species the beginning of the teleoconch (subsequent to the transitional structure) displays a pattern of oblique diverging grooves, the smooth surface is likely to be a derived condition. The rough pattern is furthermore not unique for *Helicina*, it can be observed in different genera worldwide (personal observation), the only otherwise illustrated example is given for an Australian species of *Pleuropoma* Möllendorff, 1893 by Stanisic (1997). The relevance of the structures for revealing relationships remains doubtful, especially due to the problems in the classification of the Central American mainland species (see below). Nevertheless, since the two traits in the Costa Rican species are paralleled by other similarities, although also with intergrades (e.g., shape of the teleoconch, details of the female reproductive system, degree of sexual dimorphism), it may be of importance as a supporting characteristic on a smaller scale.

The distinct transitional structure (youngest portion of the teleoconch) is not developed in all taxa. It is present in all Costa Rican species of *Helicina* and the Jamaican *Helicina neritella*, *Pyrgodomus* and *Alcadia* (*Microalcadia*). In *Lucidella* (*L. lirata* and *L. aureola*), the final pattern of the teleoconch starts directly at its origin. The same applies to *Angulata* in which the embryonic pattern is even identical to that of the teleoconch. The shells available for *Alcadia*

major were all eroded. The study of the figures given for *Helicina umbonata* Shuttleworth, 1854, *H. rhips* Thompson, 1982 and *H. liobasis* Thompson, 1982 by Thompson (1982) show a similar situation as in *Lucidella* and *Angulata*. With the exception of *Alcacia* (*Microalcacia*), the absence of the transitional structure is always combined with a spiral sculpture of the teleoconch, whereas in the other species follows an oblique or irregular pattern. Because the transitional structure in *Helicina* looks like a preliminary stage of the pattern of the oblique diverging grooves produced under different growth conditions (slower or faster), a similar effect simply would not become apparent in a spiral pattern. The lack of knowledge of the life history of Helicinidae reduces possible explanations for the interpretation of the structures. Especially the example of *Helicina umbonata* and related species (verified in its generic position by embryonic shell structures) renders this explanation likely. The systematic relevance of this characteristic by itself is therefore not suggested here, only its occurrence in combination with the pattern of the teleoconch.

Shell and Soft Body Color

Like shell characters, the color of shell and soft body are believed to reflect directly the result of selective processes by the environmental conditions. For example, a study by Johnson (1959) on *Helicina orbiculata* showed that the percentage of a lighter or darker color phase within a population is correlated to the color of the soil and obviously controlled by predation. The color is inconspicuous for species dwelling in the leaf litter, such as *Lucidella lirata*, *Alcacia hojarasca*, and *A. boeckeleri*, which are in fact more or less uniformly brownish or greyish colored. The color of *Pyrgodomus microdinus* supports the camouflage of the shell on rock surfaces. All Costa Rican species of *Helicina* for which the habitat is reported are arboreal. It is known from various examples of different families of land snails, for example, *Liguus* (Orthalicidae), *Amphidromus* (Camaenidae), and *Cepaea* (Helicidae) that colorful and varied patterned or the exceptional greenish shells seem to camouflage the individuals best. In fact all arboreal species investigated have this appearance, but it is realized in two different ways:

(1) heavy, colorful shells, which are more or less variable in their color, the mantle surface is usually unicolored: *Helicina funcki*, *H.*

pitalensis, *H. beatrix*, *H. talamancensis*, *H. punctisulcata cuericiensis* n. subsp. (?*H. echandiensis* n. sp.).

(2) slight, nearly transparent shells, except for the colored outer lip, the mantle surface is variously spotted: *Helicina tenuis*, *H. escondida* n. sp., *H. gemma*, *H. monteverdensis* n. sp., *H. chiquitica*.

Thus the development of the remarkable color patterns on the soft bodies of certain species closely depends on the thickness and structure of the shell. The best example is given by *Helicina tenuis* and *H. beatrix confusa*, which nearly equal each other in volume (females), but the shell weight of *H. tenuis* amounts to only $\frac{3}{5}$. Because the arboreal life seems to require a color as described above, the obvious physiological possibility of replacing the shell color by mantle pigmentation first makes the evolutionary development of thin shells possible. This could represent an adaptation to a limited availability of calcium carbonate due to the geological conditions in Costa Rica. *Helicina escondida* n. sp. and *H. funcki* are similar to each other with respect to the presence of greenish specimens besides strongly red tinged (shell) individuals in *H. funcki* or variously spotted (mantle) individuals in *H. escondida* n. sp. *H. chiquitica* represents an exception in so far as most individuals are nearly unicolored black. This may be related to the small size of the species, because in the individuals of *H. monteverdensis* n. sp. from Mirador Gerardo, contrary to the larger ones from Monteverde, the dark share of color prevails. Small juveniles of *H. funcki* are darkly mottled too.

In the single case of *Helicina talamancensis*, the color of the head-foot seems to be characteristic for the species. Assuming the thickness and transparency of the shell to be species-specific, the presence of a color of the soft body as described above is also characteristic because it is shown to be closely correlated with shell conditions.

Internal Shell Structures: Axial Cleft and Muscle Attachment

The absorption of the internal whorls of the spire is a common feature of the families Neritidae, Ceresidae, Proserpinidae, and Helicinidae, which had been described for the latter two families for the first time by Bland (1854). Solem (1983), while studying 15 different species of Helicinidae (worldwide, but not

specifically mentioned), established a relation between the length of the axial cleft and the number of whorls, that is, the length increases with the number of whorls. The total range is about $\frac{1}{2}$ to nearly $\frac{3}{4}$ of a whorl, and the length of the axial cleft was shown to be species-specific (five specimens of each of two species investigated). His results for *Proserpina* Sowerby, 1839, and *Ceres* Gray, 1856 (in both nearly $\frac{1}{2}$ of a whorl), differ from the description of the respective families given by Thompson (1980), with Ceresidae being about $\frac{1}{10}$ of a whorl and Proserpinidae about $\frac{3}{4}$ of a whorl. Thompson incorporated this characteristic in his considerations of systematic relationships between the families.

For the Costa Rican material, the present investigation confirms the constancy of the length of the axial cleft for different taxa, but the relation of the number of whorls to the length of the axial cleft cannot be sustained. It may be illustrated at two examples: *Helicina punctisulcata cuericiensis* n. subsp. has $3\frac{5}{8}$ whorls, with an axial cleft of $\frac{1}{2}$ whorl (Fig. 91), whereas *H. gemma* has 4 to $4\frac{1}{8}$ whorls, with an axial cleft of about $\frac{3}{8}$ whorl (Fig. 163). For *H. beatrix riopejensis* n. subsp., shells of both sexes are figured (Fig. 133) that differ in $\frac{1}{2}$ of a whorl, but the axial cleft amounts the same, here $\frac{3}{8}$ of a whorl. The second example, furthermore, shows that a relation of whorl count to the length of the axial cleft is actually in contradiction with the species-specificity, because most species of Helicinidae exhibit a sexual dimorphism in size that is accompanied by a difference in whorl count of females and males. This fact escaped the attention of Solem (1983), but it was noted by Baker (1928).

On the contrary, the length of the axial cleft seems to be characteristic for certain systematic units as the data given by Thompson (1980) suggests, although the differences between his data and Solem's (1983) remain to be checked. From the present investigation, it can be seen that *Lucidella lirata* remarkably diverges from the species of *Helicina*, the axial cleft is $\frac{1}{4}$ to $\frac{1}{2}$ whorl longer than in all species of *Helicina* studied. Also, with respect to the attachment of the right retractor muscle exclusively on the penultimate whorl, the species differs from *Helicina*. The examination of *Lucidella aureola*, the type species of *Lucidella*, revealed similar conditions (Figs. 265, 322). The same is true for *Schasicheila*, in which an axial cleft shorter than $\frac{1}{2}$ whorl is

always combined with the prominent right muscle broadly attached only on the body whorl. According to Baker (1925), the axial cleft of the primitive genus *Hendersonia* Wagner, 1905, encompasses nearly one whorl. In all species of *Helicina* studied, the attachment of the right muscle corresponds to the beginning of the axial cleft and crosses the inner suture and therefore encompasses both whorls.

Within the Costa Rican species of both subgenera of *Helicina* the length of the axial cleft varies from $\frac{3}{8}$ to $\frac{1}{2}$ of a whorl. In species of a very similar shell shape it may differ (e.g., *H. pitaisensis* – *H. tenuis*) or be of about the same length (e.g., *H. monteverdensis* n. sp. – *H. chiquitica*). The subspecies *H. beatrix riopejensis* n. subsp. represents a difficult case: it closely resembles *H. beatrix* to which it is tentatively assigned, but the length of the axial cleft is like in *H. gemma* and unlike *H. beatrix*.

Embryonic Shell

Previous to this investigation structures of the embryonic shell of Helicinidae were only applied twice for systematic considerations. Clench & Jacobson (1971) stressed features of the embryonic shell to exclude the subgenus *Striatemoda* Baker, 1940, from the Cuban genus *Emoda* H. & A. Adams, 1856. In a subsequent contribution on the genus *Alcadia* by Boss & Jacobson (1973), the embryonic shell surface is included in the descriptions of various species, but its importance has not been recognized by the authors. Their descriptions are inadequate for a comparison with results gained by SEM studies. Finally, Thompson (1982) successfully used the feature to differentiate the genera *Alcadia*, *Helicina*, and *Lucidella* by investigation of the respective type species.

The results of the present study confirm the applicability of embryonic shell structures for higher systematics in Helicinidae. Furthermore, the significance of embryonic shell features is not only justified by considerations about their conservative nature but verified by well-founded parallel changes in the female reproductive system in all species investigated. The rearrangement of certain subgeneric units of *Alcadia* provides a convincing example. Additional genera (*Eutrochatella*, *Schasicheila* and *Angulata*, newly raised to generic level) can be charac-

terized by their special embryonic shell structures. The close relationship of *Pyrgodomus* to *Eutrochatella* is confirmed. Within the subgeneric level of the genus *Helicina*, embryonic shell structures show high similarities or may vary within a single species to the same degree as between different species (e.g., *H. montevertensis* n. sp.) so that it can only be occasionally used as a distinguishing characteristic. Among the Costa Rican species, for example, only *H. talamancensis*, *H. beatrix*, and *H. beatrix confusa* exhibit relatively smaller pits with a more prominent smooth surface.

Implications of the embryonic shell structure on relationships of the different groups within the Helicinidae are by far less obvious and the following examples provide certain evidence that the similar structures are not always homologous developments. The pitted structure of the embryonic shell is known for the genera *Helicina*, *Lucidella* (pits less regularly arranged) and Australian species of *Pleuropoma* (similar to *Helicina*) (Stanisic, 1997), but, with respect to complex characters of the female reproductive system, *Helicina* represents a derived condition compared to *Lucidella*, and the genera of the Australasian region (see female reproductive system, Bourne, 1911). Furthermore, the pitted embryonic shell seems to be absent in primitive members of the family, such as *Hendersonia occulta rubella* (Green, 1832) (personal observation). Studies on embryonic shell structure of other gastropods also point to the difficulties to distinguishing homologous developments (e.g., Ponder & Lindberg, 1997).

Contrary to the structural similarity among closely related species, size provides more information. Size differences of the embryonic shell have not previously been studied for Helicinidae. According to the measurements of the Costa Rican species, size seems to depend on two main factors: (1) the size of the species, and (2) the altitude of the locality of the individuals.

(1) The diameter of the embryonic shell would best be compared with the shell volume, but because this information is not available for all species, it is compared with shell height as well as with the minor diameter of the shells (Figs. 331, 332) to consider the deviations due to different diameter-height-relations, especially for the species of *Lucidella*, *Alcadia* (*Microalcadia*) and *Pyrgodomus*. The embryonic shell size increases with the shell

size, although deviations from this general trend are remarkable. On one hand, it is explained by a certain species-specificity of the embryonic shell size as is for example shown for *Helicina chiquitica* or *H. montevertensis* n. sp.; in the latter species embryonic shell size along with other arguments could be used to distinguish the species. On the other hand, the influence of the altitude (see below) interposes with the relation to shell size. With respect to higher systematics within the family, first data for *Lucidella* and *Eutrochatella* suggest that in these genera (and related like *Pyrgodomus*), the embryonic shell size is relatively smaller than for example in *Helicina*. The specimens investigated for *Lucidella aureola* equal *Helicina gemma* in size, but the embryonic shell is about 285–335 μm smaller, those of *Eutrochatella pulchella* equal *Helicina beatrix confusa* in size, the embryonic shell is about 330 μm smaller.

(2) Since the size of the embryonic shell also seems to reflect a certain species-specificity and not only the influence by the shell size, the measurements of the embryonic shell were directly compared to the altitude (and not as a relation to shell size), but a similar diagram for shell height and diameter to altitude is given to show the general independence of shell size and altitude (Figs. 333, 334). The diagram illustrates a slight increase of the embryonic shell size at higher altitudes independently of the species within the representatives of *Helicina* and also for *Alcadia* (*Microalcadia*), although the results for the latter subgenus are more suggestive in manner than supported by sufficient data. On species level, an increase of the size of the embryonic shell with the altitude is clearly shown for *Helicina funcki* and *H. gemma*.

Faced with a virtually complete absence of data about the natural history of Helicinidae, the results cannot be discussed in this context. The knowledge is limited to a single description of deposited eggs for the species *Viana regina* (Morelet, 1849), which is cited from the observation of a Cuban malacologist by Clench & Jacobson (1968). It seems that these eggs were calcified, because the observer had to break them to examine the embryonic shell. Furthermore, it is known that eggs are released from the ovary into an egg sac at the very beginning of the primary oviduct. In histological sections, these eggs can occasionally be observed in the primary oviduct and in the ascending limb of the V-organ,

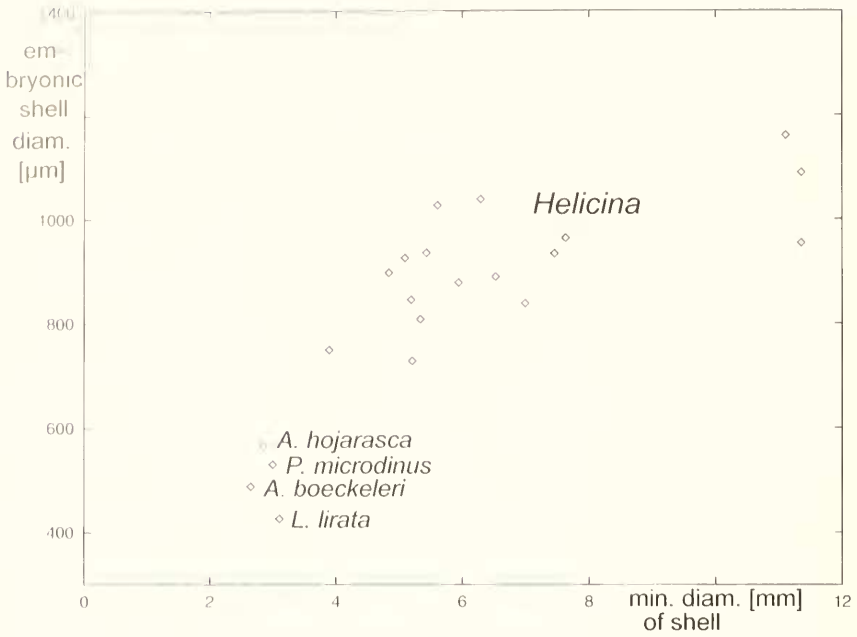


FIG. 331. Relation of embryonic shell diameter to minor diameter of the shell for Costa Rican species (all species included for which measurements of the embryonic shell were given).

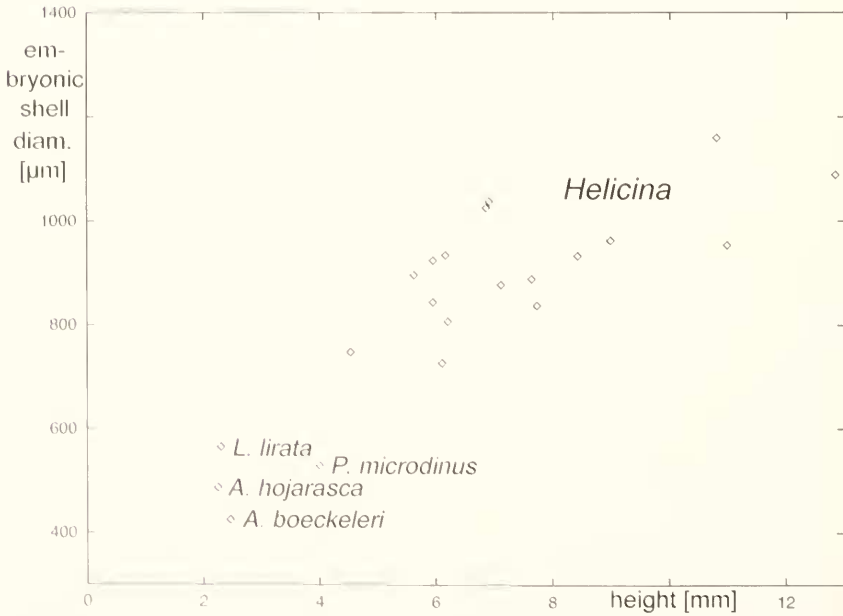


FIG. 332. Relation of embryonic shell diameter to shell height for Costa Rican species (all species included for which measurements of the embryonic shell were given).

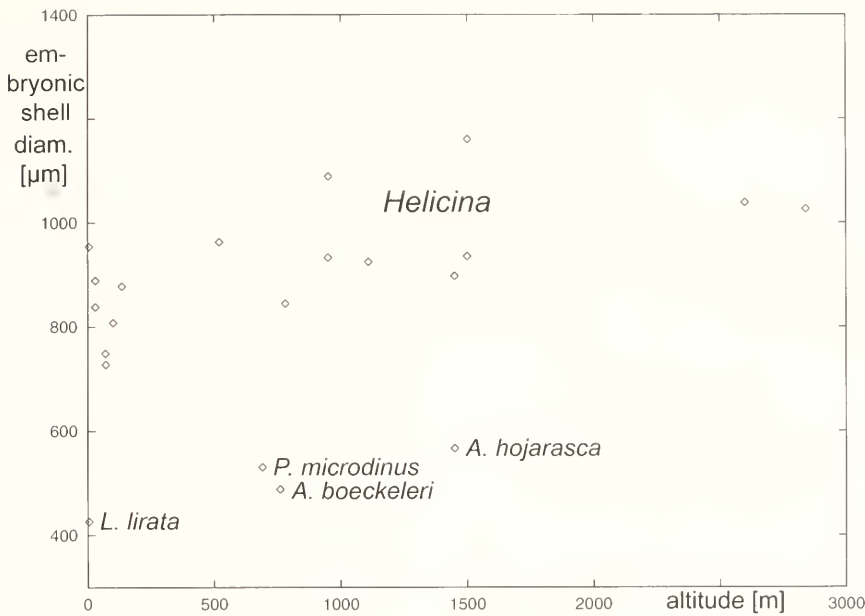


FIG. 333. Relation of embryonic shell diameter to the altitude of the site of the Costa Rican species (all species included for which measurements of the embryonic shell were given).

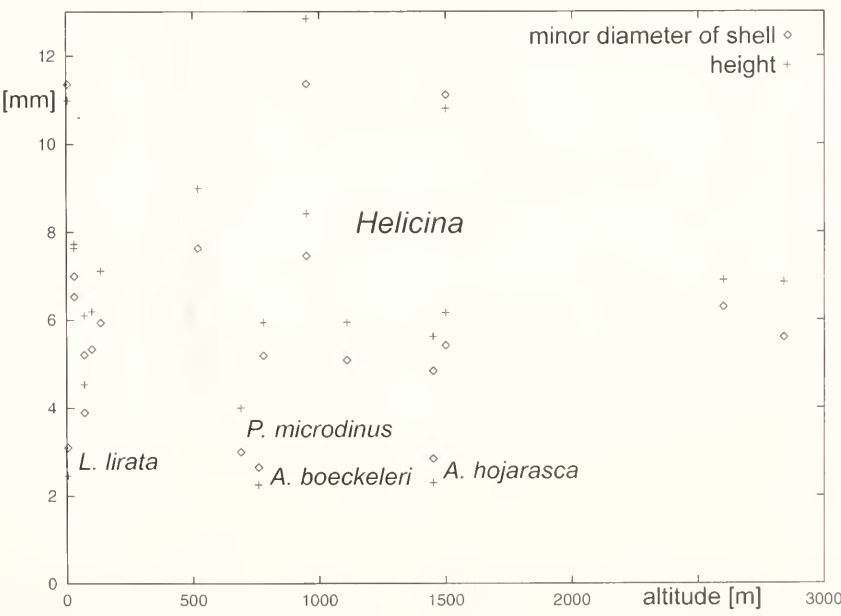


FIG. 334. Relation of shell height or minor diameter respectively to the altitude of the site for the species included in diagram Fig. 333.

but distal to this portion (and therefore fertilized) eggs were never seen or reported by other authors.

Operculum

Wagner's classification represents the first attempt to incorporate the characteristics of the operculum to a large extent. For this reason, the opercula of other than the Costa Rican species are not repeatedly described and discussed. As for shell characteristics, the features on which the operculum closely depend, subsequent studies, including the present one, showed the high flexibility for adaptations to environmental requirements by cases of convergent developments reflected in necessary rearrangements of different taxa. For the genus *Alcadia* from Cuba, Boss & Jacobson (1973) compared the calcification of the operculum in relation to habitat. In arboreal species, the calcareous layer is thinner than in ground-dwellers, the latter possibly requiring stronger protection against small predators.

Aspects of the operculum were successfully applied to recognize and characterize the primitive members of the family by strong traces of a retained paucispiral instead of a concentric condition (Wagner, 1907–1911; Baker, 1922a).

The opercula of the Costa Rican species of *Helicina* are very uniformly developed. Deviations in shape are due to the different shape of the aperture of the shells, for example, the operculum of *H. funcki* is broader than that of *H. beatrix*, because the whorls of the former species increase more rapidly in size. The opercula of *Alcadia hojarasca* and *A. boeckeleri* do not differ from those of *Helicina* species, except for the more irregularly S-shaped columellar edge, reflecting the condition of the strongly rounded periphery of the shells. This illustrates in exemplary fashion that the similarity in the operculum does not necessarily reflect a close relationship between the taxa, especially in the case of certain subgeneric units of *Helicina* and *Alcadia*.

Radula

Because radular characteristics strongly influenced the systematic concepts for the Helicinidae, these structures were described and figured in some detail within the species accounts.

The interpretation of the capituliform complex requires some remarks, because it has caused some past confusion. Originally, Troschel (1856–63) described the accessory plate as a basal appendage, which is always fused with the tooth, but appearing somehow subdivided. Baker (1922a) recognized two plates and paid much more attention to the form of the accessory plate and the point and way of the overlapping of both teeth. His figures give the impression of separate teeth. The peculiar reflexed wing of the accessory plate was corrected in its interpretation by Baker (1926, 1928) as a deposit cementing the two plates together instead of being a kind of a cusp. The plates are said to break upon separation in certain groups of species, whereas in others they "pull apart easily enough". This correction obviously escaped the attention of subsequent authors. Adopting Baker (1922a), Thompson (1980, 1982) still incorporates the characteristic of the wing or reflection of the accessory plate enveloping the end of the comb-lateral for his phylogenetic considerations. This wing is actually not visible in his SEM figures, because it was a misinterpretation of optical microscopic investigations. Stanisic (1997) states that, contrary to certain overseas (= neotropical) species, the comb-lateral and the accessory plate of the Australian species of Helicinidae are always fused together. But in this respect, his SEM figures do not differ from those of neotropical taxa, for example, the Costa Rican species. In natural conditions, the two plates are fused together.

As previously stated, data of this study were gained by SEM-investigations. Despite the great advantages of the higher resolution revealing more exactly the dentition of the marginals and information from the three-dimensional arrangement, the method is accompanied by some disadvantages. On account of the very complex structure of the radula, the numerous marginals always overlap each other, especially the outer ones, rendering an exact count impossible. To a lesser extent, a similar problem exists in analyzing the number of transverse rows, because, especially in small or poorly preserved specimens, the preparation procedure and the necessary positioning may result in losses of parts of the whole ribbon. In optical microscopy especially, the first point simply becomes obsolete by the transparency of the radula. Nevertheless, here the SEM-method is pre-

ferred because drawings from the light microscope reflect rather the interpretation of the author than the real and hereby comparable structures as argued above.

In all Costa Rican species of *Helicina*, the radula displays nearly the same amount of intraspecific and interspecific variations. The only specific differences clearly documented were found in the dentition of the comb-lateral of two species, *H. escondida* n. sp. and *H. chiquitica*. In these species, the number of cusps is constantly strongly reduced or increased, in the former species, the size of the cusps is remarkably enlarged towards the centrals. The differences described for the change in the number of cusps on the marginals are in most cases likely to be related to the size of the species. Evidence is provided by the differences in the subspecies of *Helicina beatrix*. Furthermore, all small-sized species (*Helicina chiquitica*, *Lucidella lirata* and *Alcadia (Microalcadia) hojarasca*) convergently possess an increased number of denticles on the comb-lateral.

Stanisic (1997), while studying Australian species of the genus *Pleuropoma*, in which the radula in general apparently does not differ remarkably from those shown in this study, points out specific differences of the comb-lateral for certain species analogous to those observed for *Helicina escondida* n. sp. and *H. chiquitica*, and in the cusps of the centrals as well. He relates the divergence in the radula to the habitats of the species – arboreal, ground-dweller and limestone-associated.

The results and interpretation of Stanisic (1997) agree with my own conclusions of seeing the features of the radula more in the light of speciation and adaptations to the substratum the respective species feed on and thus to be subject to convergent development rather than providing a conservative structure useful to indicate phylogenetic relationships. This concept does not exclude the possibility that a certain radiation resulted from the colonization of a special habitat (e.g., *Eutrochatella* and related taxa of the West Indies on calcareous rocks), which is therefore characterized by the obviously necessary adaptation of the radula (e.g., the reinforced T-shaped lateral). On one hand, the fact of the rearrangement of certain groups of Baker's system characterized by radula characteristics provides evidence in itself. On the other hand, additional examples can be given for convergent developments. Boss & Jacobson (1973) and

Thompson (1982) had recognized the diverging radula of *Alcadia major* (T-shaped laterals and other features approaching the "vianid" radula instead of the "helicinid" radula typical for other subgroups of *Alcadia*) but hesitated to comment on this "not matching" fact. Because *Alcadia major* lives on "rock bases" (Baker, 1934a) like other species with a "vianid" radula (e.g., *Eutrochatella pulchella*, *Pyrgodomus microdinus*), a convergent foraging structure is very likely and is here favored as an explanation. Outside of the family Helicinidae, a convergent development of the "vianid" radula had already been proposed and accepted by Thompson (1980), namely for the Proserpinidae.

Morphometry and Sexual Dimorphism

The morphometric differences were discussed to some extent in the species account and proved to be useful on the species level, for example, to judge the status of certain subspecies (*Helicina funcki costaricensis*, *H. tenuis pittieri*). Furthermore, a relation to the altitude seems to be specifically different, but data were sufficient only for a few species. A decrease in size at higher altitudes (*Helicina funcki* and *H. gemma*) has also been reported for the Mexican species *H. fragilis elata*, *H. zephyrina zephyrina* and *Pyrgodomus microdinus abditus* by Baker (1928). The study also shows that morphometric analysis of Helicinidae always has to take into account the considerable effects of sexual dimorphism.

Sexual dimorphism in Helicinidae has been known for a long time, but, with very few exceptions, it has never been subjected to detailed studies. Probably the most frequently cited example is the different shape of the shells of both sexes in *Viana regina*, with the males being characterized by a deep notch in the upper outer lip, a fact that was first recognized in this context by L. Pfeiffer (1856a). Wagner (1910b) considered the subject theoretically because he did not have anatomical material available. The species discussed by him were not studied here. Baker (1925) published the first accurate data for differences in size for *Hendersonia occulta rubella*. Although he selected extremes for the measurements expecting the females to be larger, the difference in volume interpolated from his data amounts to about 2% less for the males and both sexes intergrade. Baker (1926) mentioned only the relationships of females to

males of the specimens he had studied anatomically. Baker (1928) analyzed some Mexican species morphometrically, but, with minor exceptions, the number of specimens for each station was limited. According to his results, the sexes intergrade considerably in shape and size, but the shells of males increase more rapidly in diameter resulting in fewer whorls ($\frac{1}{4}$ to $\frac{1}{2}$) and a more depressed shell shape, when sexual dimorphism is developed. The genus *Schasicheila* seems to encompass species with sexual dimorphism (*S. alata*, females > males) and another with intergrading sizes (*S. misantlensis* Fischer & Crosse, 1893, females = males). In later studies on the Jamaican malacofauna, Baker (1934a, b) provided further information, but unfortunately did not include numerical data or the sample size. According to him, all species examined of *Eutrochatella* *E. pulchella*, *E. tankervillii* (Gray, 1824), *E. nobilis* (C.B. Adams, 1852) and *E. costata* (Gray, 1824) – have males larger than the females, whereas the closely related genus *Pyrgodomus* (Baker, 1928: *P. microdinus abditus*, examination based on several shells) shows the reverse relation. Species of *Lucidella* show all possible relations (<, >, =), and *Helicina* and *Alcadia* are similar in having larger females. A single exception for *Helicina* is given in "*H. (Angulata) rhynchostoma ernesti*" von Martens, 1873 (Baker, 1926), but this species requires re-examination regarding its systematic affinities.

The data on sexual dimorphism of this study represent the most comprehensive approach to date to analyze the phenomenon for a selected group of species. Against the background of limited material available, the newly developed method of removing the soft body with only minor damage to the shell provides a valuable tool, which made the analysis possible. All species measured exhibit a sexual dimorphism in size of the shell, with females averaging larger than males. Differences are smallest in *Lucidella lirata* (percentage of male's volume about 92%), increase in *Helicina funcki* and *H. pitlensis* (about 80–85%), *H. tenuis*, *H. echandiensis* n. sp. and *H. escondida* n. sp. (about 75–78%) to the greatest values in *H. beatrix*, *H. talamancensis*, *H. gemma*, *H. monteverdensis* n. sp. and *H. chiquitica* (about 61–67(–72)%). This grouping is paralleled by similarities in shell shape, teleoconch surface structure and details of the female reproductive system, suggesting a certain value of the degree of sexual dimorphism

with respect to systematic affinities. The group with the highest differences shows furthermore that the dimorphism is independent of the size of the species, because the extrema (*Helicina talamancensis* and *H. chiquitica*) differ in volume by a factor of about 7.

The observation by Baker (1928) that in case of a sexual dimorphism males are more depressed, that is, relatively larger in diameter, could not really be confirmed by the present study. For all species, the different measurements were tested in various relations to each other and no significant differences for both sexes were found. For the relation of height to diameter (here minor diameter), deviations between females and males for acceptable sample size usually range approximately 1% or less for all species, highest differences amount up to 3–4% for very few populations. In more populations, the relative diameter was larger in males than in females, but examples for a reverse relation were found likewise in nearly all species.

The morphometric comparison of different populations clearly demonstrates a certain variability of size for most species and indicates that investigations of the sexual dimorphism will only work with individuals originating from the same population.

The knowledge of the range of size variations within a species due to sexual dimorphism allows a much better judgement of the determination of single specimens, for example, type specimens, and morphometric differences applied for the separation of species or subspecies.

Female Reproductive System

When revising the contributions on systematics of the Helicinidae with respect to the anatomy, especially genitalia, all authors agree in the following: "... but once they [anatomical structures] evolved very little differentiation of these organs and structures occurred with further radiation of subfamilies and genera" Thompson (1982: 5), or more strictly "This emphasizes the conclusions of Bourne (1911: 777) and Baker (1926: 35) that the general uniformity of the genitalia of the Helicinidae makes them useless for diagnostic purposes" Boss & Jacobson (1974: 6).

The first comprehensive study on the anatomy of Helicinidae based on several species worldwide, combining both dissections and histological studies, was carried out by

Bourne (1911). A similar study was provided only for the primitive species *Hendersonia occulta rubella* by Baker (1925). All previous contributions considered the one or the other detail of different species (Isenkrahe, 1867: first rough anatomy of *Emoda pulcherrima titanica* (Poey, 1851); von Ihering, 1877: nervous system of *Pleuropoma beryllina* (Gould, 1847); Bouvier, 1886: nervous system of *Angulata brasiliensis* and *Emoda sagraiana* (Orbigny, 1842); Thiele, 1902: male reproductive system of *Waldemaria japonica* (A. Adams, 1861); Thiele, 1910: female reproductive system of *Helicina kubaryi* [*nomen nudum*?]). Baker (1926, 1928) studied several American species with emphasis on the genitalia. He clearly states that his intention of finding similar clues for systematic affinities, as in the radula, partially failed, not exclusively because of the considerable uniformity of the structures, but also on account of the scanty and poorly preserved material. Therefore, his contribution is a valuable collection of descriptions for several anatomical features, but the nearly complete absence of conclusions and discussions renders it subject to misinterpretations, as exemplified in the citation above. Subsequent to Baker, only Thompson (1968) described the genitalia of his new genus *Ceochasma* and provided a detailed anatomical study on two species representing the related families Ceresidae and Proserpinidae (Thompson, 1980).

The present anatomical studies focused on the investigation and comparison of the female reproductive system since, on one hand, the discovery of important deviations from the present knowledge promised information relevant for phylogenetic purposes contrary to former assumptions, but on the other hand, it required the re-examination of previously studied species/genera and the assessment of data within the new context.

The study of the Costa Rican species of *Helicina* revealed that all species are similar in the monaulic condition of the female reproductive system. This result is in contradiction with all previous anatomical studies (diaulic system), especially those of Baker (1926) for various Central American species of *Helicina*. Baker (1926) assumed the vaginal opening to be inside the duct of the hypobranchial gland also discharging into the mantle cavity. This is reflected in his figures of the female systems (e.g., fig. 9, *H. orbiculata*). In fact, the hypobranchial duct and gland is closely associated

with the apical complex of the female reproductive system, partially enveloping these structures dorsolaterally. In dissection, their separation is not always easy, but the study of histological serial sections finally confirmed the absence of any connection of the reception chamber or associated structures to the hypobranchial duct. Other Central American species, such as *Helicina amoena*, *H. turbinata*, and *H. orbiculata*, the latter also studied by Baker (1926), also constantly lack the provaginal opening. Until more knowledge is available, these results together with the only vague presentation of the provaginal opening in Baker's figures lead me believe that all Central American mainland species commonly referred to *Helicina* are monaulic, that is, that they properly belong to that genus.

Reexamination of several other species studied by Bourne (1911) and Baker (1926) and additional type species of higher systematic units revealed a much higher structural diversity than previously documented. For example, contrary to the results of Bourne (1911) *Eutrochatella pulchella* was found to be monaulic. For *Lucidella lirata* as well as for *L. aureola*, an additional sac on the pallial oviduct for sperm storage was discovered. Furthermore, the receptaculum seminis on the descending limb of the V-organ described by Baker (1926, 1928) turned out to be a misconception. These results add several peculiarities for *Lucidella* and differentiate it more strongly from other genera. The characters of *Schasicheila* (Baker, 1926, 1928) and *Alcadia* (Bourne, 1911) were confirmed.

The changes in the female reproductive system are paralleled by consistently different structures of the embryonic shell and add valuable features in the characterization and differentiation of genera and subgenera, for example, *Alcadia* from *Helicina*. Furthermore, certain changes can be assessed in the direction of the development. The basal members of Helicinidae, such as *Hendersonia occulta rubella*, possess a diaulic system. The basal position is reliably founded on the paucispiral conditions of the operculum and the presence of the vestigial right auricle. The monaulic condition is clearly the derived condition. Furthermore, the diaulic state seems to prevail in most of the genera. Assuming the results of Bourne (1911) for this part to be correct, Australasian species are diaulic as well. At least *Aphanoconia pachystoma ponsonbyi* (E.A. Smith, 1884) from Papua New Guinea,

was re-examined and the structure could be confirmed.

The mon- or diallic state is expected to be related with functional consequences. But although the morphological structures are fairly well documented, knowledge of functional aspects is limited to the interpretation of morphological features, because other data are not available. Bourne's (1911) observations were not homogeneous for the different taxa and point in different directions. The presence of sperm in the posterior part of the pallial oviduct, the bursa copulatrix, and the receptaculum seminis of *Alcadia hollandi* suggested that the pallial oviduct serves as the copulatory canal. By the way of contrast, two Australasian species of *Aphanoconia* had sperm within the provaginal duct and the provaginal sac, favoring the reception of sperm through this opening. Baker (1925) assumed the provaginal opening to receive the male products in *Hendersonia occulta rubella*, as did Thompson (1980). The monaulic structure only allows the reception of sperm through the pallial oviduct, and therefore demonstrates the physiological possibility. Following this consideration, the provaginal opening could also be functionally vestigial, at least with respect to the reception of sperm, in species with this opening. Under the morphological conditions of *Lucidella* for example (Figs. 270, 324), the reception of sperm through the vagina would require a downward movement to reach the posterior extended portion of the oviduct and its lower appendage, in which sperm were found. The function of the various different structures for sperm storage is even less understood. In most of the different systems there are three structures that are found to be used simultaneously (receptaculum seminis, bursa copulatrix, provaginal sac, ?parts of the pallial oviduct, the appendage of the pallial oviduct or other analogous developments). These aspects remain subject to further studies, possibly ultrastructural analysis.

The variability or specificity of characteristics of the female reproductive system at the species level was studied in detail for the Costa Rican species. Here the applicability is limited, as may be expected for characters useful for higher systematics. Differences mainly occur in the shape and size of the bursa copulatrix and the provaginal sac, as well as in the relation of the apical complex to the pallial oviduct. The latter feature seems to depend more on the size of the species, because the apical

complex is not proportionally larger in larger specimens, but the absolute distance to the mantle edge is longer, for example, *Helicina funcki*, *H. pitalensis*. The shape of accessory structures is nearly independent of the developmental stage. Baker (1926) observed that lobules of the bursa copulatrix of immature *Helicina convexa* L. Pfeiffer, 1849, were almost as well developed as those of adults. Dissections of immature *Helicina funcki* confirm this assumption (Fig. 19, right drawing). The main changes connected with maturation take place in the development of the ovary that finally covers large parts of the visceral portion and an enormous thickening of the epithelium of the pallial oviduct (Bourne, 1911; personal observations). Furthermore the content of the accessory structures (empty or filled) does not remarkably influence the shape. Therefore the deviations illustrated are more likely due to intraspecific variability rather than different physiological conditions. Similar to the radula for some species, a certain peculiarity can be recognized, for example, the lobules at the upper end of the provaginal sac of *Helicina tenuis*, the elongated lobes of the bursa copulatrix of *H. funcki*, similarly developed in specimens from Panama (Baker, 1926).

Arrangement of Central American Mainland Taxa

Except for the single species *Pyrgodomus microdinus* and *Lucidella lirata*, the main part of the Costa Rican Helicinidae – namely the species of *Helicina* – was controversially classified and shifted to subgroups of *Helicina* or *Alcadia*. Because this confusion is characteristic for the two genera involving most of the American mainland species and a considerable portion of the Caribbean species, it must be treated to some extent. Subsequently, aspects of the remaining Central American mainland genera will be discussed.

The Genera Helicina and Alcadia

In the following, the different classifications of *Helicina* and *Alcadia* and related subgenera proposed in literature will be presented, critically summarizing the main distinguishing characters of the groups that were stressed by the authors. The respective systematic position of the Costa Rican taxa is indicated. Additionally, all relevant

subsequent contributions on the systematic classifications will be discussed. Finally, the differentiation and characterization of the genera and subgroups and necessary rearrangements will be proposed according to the morphological characters and their partially deviating assessment outlined by this study.

Wagner (1907–1911) – mainly based on features of shell and operculum. The respective assignment of the Costa Rican species is highlighted in bold face style.

Alcadia

Subgenus: *Eucaladia* [= *Alcadia*]: Jamaica, Cuba, Bahamas, St. Thomas, St. Jan [= St. John?], Vieque, Puerto Rico, Hispaniola, French Guyana, Suriname, Brazil

Formenkreis "*Palliat*": Jamaica, Cuba

Formenkreis "*Hispida*": Cuba, Bahamas, St. Thomas, St. Jan [= St. John?], Vieque, Puerto Rico

Formenkreis "*Intusplacata*": Hispaniola

Formenkreis "*Sericea*": French Guyana, Suriname, Brazil

Formenkreis "*Incrustata*": Cuba

Subgenus: *Leialcadia* [= *Idesa*]: Cuba, Jamaica, Puerto Rico, Hispaniola, Trinidad, Venezuela, Colombia, Costa Rica, Nicaragua, Guatemala, Mexico

Formenkreis "*Megastoma*": Jamaica, Cuba, Puerto Rico

Formenkreis "*Nitida*": Cuba, Puerto Rico

Formenkreis "*Mamilla*": Hispaniola, Cuba

Formenkreis "*Bellula*": Cuba

Formenkreis "*Ampliata*": Jamaica

Formenkreis "*Tamsiana*": Trinidad, Venezuela, Colombia

Formenkreis "*Gemma*": Costa Rica, Nicaragua, Guatemala, Mexico: ***gemma***, ***beatrix***, (***fragilis***)

Subgenus: *Analcadia*: Guadeloupe, Martinique, St. Lucia, Dominica, Venezuela, Trinidad, Belize, Bonacca (island off Honduras), Nicaragua, Hispaniola, Puerto Rico, Vieque, St. Jan [= St. John?], Tortola

Subgenus *Emoda*: Cuba

Helicina

Formenkreis "*Angulata*" and "*Variabilis*": Brazil

Formenkreis "*Concentrica*": Venezuela, Colombia, Peru, Bolivia

Formenkreis "*Punctisulcata*": Mexico, Guatemala: ***punctisulcata***

Formenkreis "*Cinctella*": Mexico, USA

Formenkreis "*Tenuis*" [= *Pseudoligyra*]: Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Bolivia: ***tenuis***

Formenkreis "*Turbinata*": Panama, Costa Rica, Nicaragua, Honduras, Mexico, Guatemala: ***funcki***, ***pitalensis***

Formenkreis "*Succincta*": Mexico, Guatemala

Formenkreis "*Festiva*": Hispaniola

Formenkreis "*Euneritella*" [= *Helicina*]: Cuba, Jamaica, Grenada, St. Vincent, Guadeloupe, Dominica, Bonacca, Martinique, Trinidad, Barbados, Bermuda

The differences between *Helicina* and *Alcadia* given by Wagner (1907–1911) can be summarized as consisting mainly of shell characteristics (in *Helicina*: umbilical area always and constantly with an impressed line or groove, no periostracal hairs; *Alcadia* s.s.: typical basal notch). Furthermore, the operculum of *Helicina* only differs in a less prominent sigma-edge and a nucleus most closely approaching the columellar edge (but this is also attributed to *Analcadia*, *Leialcadia* and *Alcadia* s.s. partially). Wagner (1907–1911) adds that some species of *Alcadia* and Mexican and Antillean species of *Helicina* intergrade or only weakly exhibit the typical characters respectively.

With respect to the characteristics of the operculum, *Analcadia* differs from *Leialcadia* only in a deeper groove near the lower part of the sigma-edge, other differences apply to shell characteristics. *Leialcadia* is typically characterized by the shiny and lasting periostracum and reduced characteristics of aperture and operculum. Both subgenera lack the prominent calcareous plate of the operculum and the deep notch in the basal part of the aperture described for *Alcadia* s.s.

The "Formenkreise" were only used to summarize groups of species, they were introduced without any description or type species.

Baker (1922a) – mainly based on characters of the radula, in combination with some features of the shell and operculum.

Oligyra (tropical and subtropical America)

Subgenus: *Oligyra*: tropical and subtropical America

Section: *Oligyra* s.s.: USA, Bermuda Islands, Mexico

Section: *Succincta*: Mexico to South America: ***gemma***, ***beatrix***

- Subgenus. *Alcadia*. West Indies to South America
 Section: *Idesa*: West Indies
 Section: *Analcadia*: Antilles to Central America
Helicina (tropical America)
 Subgenus: *Helicina*: West Indies
 Subgenus: *Tristramia*: mainland [of tropical America]
 Section: *Oxyrhombus*: Central and E-Mexico to South America: ***punctisulcata***
 Section: *Tamsiana*: northern South America
 Section: *Angulata*: South America to Central America
 Section: *Tenuis* [= *Pseudoligyra*]: Mexico to Central America; South America: ***tenuis***
 Section: *Tristramia*: Mexico to Colombia: ***funcki*, *pitalensis***

According to Baker (1922a), *Oligyra* differs from *Helicina* by a well-developed wing at the accessory plate and centrals with always well-developed cusps. The operculum shows intergrading characters. Compared with *Alcadia*, the genus has a light operculum lacking the inferior point fitting in the corresponding notch in the basal outer lip, and A- and B-central do not exhibit heavy backs. It was later maintained that *Oligyra* and *Alcadia* belong to two diverging lines of evolution. It would, however, be extremely difficult to name any very definite characteristics for their separation.

Succincta differs from *Oligyra* in the tendency of reduction of the cusps of the A-central, whereas A- and B-central of *Oligyra* are with well-developed cusps. Additionally, the shell is more globose, and marginals show a wing-like expansions below the tips (otherwise strictly lingulate).

According to Baker (1923) the centrals of the radula of *Analcadia* resemble those of *Oligyra* s.s., but shell characters approach those of *Alcadia*, suggesting *Analcadia* as a subgenus between the subgenera *Oligyra* and *Alcadia*. The radula of *Oligyra* (*Alcadia* – section: *Idesa*) *rotunda* is said to agree with *Alcadia* s.s. in the centrals and with *Sericea* or *Analcadia* in the comb-lateral.

Tristramia differs from *Helicina* in strictly lingulate marginals (not sickle-shaped with lateral wings near tips), a lacking shelf-like projection bearing the cusps on the A-central and a differing accessory plate (operculum and comb-lateral are equal). The differences between *Oxyrhombus*, *Tamsiana*, *Angulata*,

Tenuis, and *Tristramia* include shell characteristics (presence or absence of a spiral striation, periphery angular or not) and radula characters not worth mentioning.

All the radula differences within *Helicina* and *Oligyra* (because the main difference “the wing” was a misinterpretation) become reduced to minor deviations in cusp development (presence and shape) on centrals and the comb-lateral and the arrangement and an increase in the number of the cusps on the marginals (more on tip or laterally).

The author erroneously recognized the “Formenkreise” of Wagner (1907–1911) as relevant supraspecific taxa and, by doing so, made them nomenclaturally available (Zilch, 1948); some became objective synonyms of older supraspecific taxa, other were synonymized, but some were accepted as sections. Because there is good reason to suppose that Wagner based the “Formenkreise” on similarities of shell characteristics, it may be said that for the taxa accepted and kept in their position, Baker only attempted to consolidate this system with questionable radula features, instead of having raised it based on these characteristics.

Baker (1926) – system modified to incorporate anatomical characters.

Helicina

Subgenus: *Helicina*

Subgenus: *Oligyra*

Section: *Oligyra* s.s.

Section: *Succincta*: ***gemma*, *beatrix***

Subgenus: *Tristramia*

Section: *Tristramia* s.s.: ***funcki*, *pitalensis***

Section: *Tenuis* [= *Pseudoligyra*]: ***tenuis***

Subgenus: *Oxyrhombus*

Section: *Oxyrhombus* s.s.: ***punctisulcata***

Section: *Angulata*

Section: *Tamsiana*

Alcadia

Subgenus: *Alcadia*

Subgenus: *Analcadia*

Subgenus: *Sericea*

Subgenus: *Idesa* (included after Baker, 1923)

Because Baker assumed the anatomy of *Alcadia* s.s. was distinct from *Oligyra* (he studied *Analcadia* and *Sericea*, but did not have adequate material of *Alcadia* s.s. and only very critically interpreted the [correct] figure given by Bourne, 1911, as generalized), he raised *Alcadia* again to generic level and pointed to further investigations to show the

exact line of demarcation between *Oligyra* and *Alcadia*. He stated that shell and radula characters of *Succincta* (*Helicina* (*Succincta*) *cacaguelita* Pilsbry & Clapp, 1902, examined) approach those of *Alcadia*, but the anatomy appears closest to that of the subgenus *Tristramia* (*Helicina* (*Tristramia*) *funcki* examined).

Baker pointed out that anatomical and shell characteristics of *Helicina* and *Oligyra* "intergrade to such an extent, that one meets considerable practical difficulty in any attempt to differentiate the two groups." Therefore, he included *Oligyra* with two sections as subgenus into *Helicina*.

When describing the anatomy of *Helicina* (*Oxyrhombus*) *cinctella*, Baker (1928) remarked that the female genital system is intermediate between those of the species of *Oligyra* and that of *H. concentrica* L. Pfeiffer, 1849 [the only representative for *Oxyrhombus* studied by Baker (1926)], although the structure of the bursa copulatrix distinctly approaches that of *Tristramia*.

Rehder (1966) discussed the systematic affinities of *Helicina bocourti* Crosse & Fischer, 1869, Honduras (formerly regarded as subspecies of *H. dysoni*, Venezuela) applying the characteristics of the radula and concluded that both species belong to the subgenus *Tristramia*, of *Helicina*, synonymizing *Oxyrhombus* and *Tristramia*, because the radula of *H. bocourti* combines characteristics of both groups. Regarding a rearrangement of the subgenus *Analcadia*, of which *H. dysoni* is the type species, to *Helicina* instead of *Alcadia*, Rehder (1966) avoided a direct statement, because he later pointed to the periostracal hairs and the development of the operculum of *H. dysoni* as characteristic of the genus *Alcadia* and mentioned his uncertainty "that radular characteristics alone can be used for subgeneric differentiation".

Boss & Jacobson (1973) revised the Cuban species of the genus *Alcadia*. Considering anatomical studies of the previous authors and combining their own results on the radula with Baker's (1922a), they pointed out that "shell morphology, together with certain features of the operculum still constitute the most reliable method of distinguishing members of the genus". They then proceed to differentiate *Helicina* and *Alcadia* mainly by the basal notch or sinus of the shell and an internal lamella and groove on the columellar edge of the operculum. Nevertheless, it remains doubtful

how they define the genus outside of Cuba, that is, the exact line of demarcation between *Helicina* and *Alcadia*, because *Alcadia* in their sense (Boss & Jacobson, 1973: 311–312) occurs on most of the West Indian islands as well as on the mainland from southern Mexico to northern South America. Actually, this distribution only agrees with Wagner's version and not with that of Baker (1922a, 1926), who attributed part of Wagner's *Leialcadia*, namely the species groups "*Gemma*" and "*Tamsiana*", to *Helicina* or *Oligyra* respectively and, by doing so, excludes *Alcadia* from Central America (but not from northern South America). Boss & Jacobson (1973) even assumed the origin of the genus to be in Central America.

Their investigation of the radula of four Cuban species (two of them type species of subgenera) and *Alcadia major* (Jamaica) revealed that it cannot be used as a diagnostic feature for *Alcadia*, at least at the present state of knowledge. Troschel (1856–63), for example, noted a different shape of the R-central in *Helicina* and *Alcadia*, but Boss & Jacobson found it to be too variable in their species studies of *Alcadia*.

Thompson (1982), clarifying the systematic affinities of the species group *Helicina umbonata* from the West Indies, used embryonic shell structures for the first time, because they are of conservative character and show little variations within species or closely related groups. When judging other characteristics for their applicability to systematics, he regarded shell and operculum as being directly affected by evolutionary pressures due to their direct contact with the environment and thus as being subject to convergence. By the way of contrast, Thompson (1982) assumes the radula as a useful, conservative morphological system, citing the studies of Baker (1922a), although it is obviously also under direct selective pressure as foraging organ, and although Thompson (1980) argues that the vianid radula (radula with inner lateral T-shaped) has convergently evolved in Proserpinidae and Vianinae for similar trophic activities.

His results with respect to the embryonic shell show that *Alcadia* clearly differs from *Helicina* s.s. Other generic units placed in *Alcadia* as subgenera are said to agree with *Alcadia* s.s., whereas some mainland subgenera associated with *Helicina* differ from *Helicina* s.s. thus requiring re-examination. Against the backdrop of the controversial ar-

rangement of subgeneric units of *Helicina* and *Alcadia*, it remains doubtful just what Thompson (1982) refers to. He does not specify any taxa or species on which he based his statement about the subgeneric taxa except for those genera within the actual scope of his study (*Helicina* s.s., *Alcadia* s.s., *Lucidella* s.s. and *Poenia*).

To summarize the present state of knowledge, it can certainly be stated, that the discrimination of the genera *Helicina* and *Alcadia* and their associated subgenera remains a controversial topic. Especially the species groups "*Gemma*" and "*Tamsiana*", the former encompassing part of the Costa Rican taxa, were shifted either to the one or other genus. Radula differences turned out to be wrong interpretations or to intergrade or vary. The features of shell and operculum most strongly and constantly influenced the classification since they actually also represented the foundation for later concepts. The anatomy has been regarded as too uniform and conservative even within the Helicinidae, except for some primitive members (e.g., *Hendersonia*). The only definite and first hint for a clear separation of the genera s.s. is given by the structure of the embryonic shell.

New Proposed Arrangement

From the results of the present study, the following arrangement is proposed for those taxa investigated. Details of the assessment of the different characteristics were discussed in the foregoing chapter. Contrary to previous attempts, emphasis is placed on differences in the female reproductive system, which agree with changes in the embryonic shell structure.

*Helicina**

Subgenus: *Helicina* s.s. (West Indies)

Subgenus: *Tristramia* (Synonyms: *Oxyrhombus*, *Pseudoligyra* [= *Tenuis*], ?"*Cinctella*") (Central American mainland): ***funcki*, *pitalensis*, *tenuis*, *echandiensis* n. sp., *punctisulcata cuericiensis* n. subsp.**

Subgenus: *Oligyra* (Synonym: *Succincta*) (Central American mainland)

Subgenus: "*Gemma*"^{***}: ***gemma*, *beatrix*, *talamancensis*, *monteverdensis* n. sp., *chiquitica*, *escondida* n. sp.**

Subgenus: *Ceochasma* (Mexico)

Subgenus: *Analcadia* (northern South America)

Subgenus: *Sericea* (northern South America)
?Subgenus: *Tamsiana* (northern South America)

Angulata (South America)

Alcadia^{***}

Subgenus: *Alcadia* (West Indies)

Subgenus: *Microalcadia* n. subgen. (Central American mainland): ***hojarasca*, *boeckeleri***

Subgenus: *Idesa* (West Indies)

* the South American taxa will be discussed, but they are only included as examples, because they were beyond the actual scope of this study

** the taxon *Gemma* is preoccupied, but considering the uncertainty of the this subdivision, it seems unjustified at present to replace the name

*** other Antillean subgenera are not considered

Helicina is characterized by the embryonic shell structured with pits arranged in concentric lines, the absence of a provaginal opening (i.e., monaulic), and an externally subdivided bursa copulatrix in the female reproductive system.

In *Alcadia*, the embryonic shell exhibits more or less strong oblique grooves and coarse, irregularly spaced radial threads. The provaginal opening of the female system is present (i.e., dialic) with an elongated provaginal duct. The bursa copulatrix is an oblong sac that is externally not distinctly lobed. Other examples included West Indian subunits (*Palliatia*, *Idesa*, and the species *Alcadia jamaicensis*, formerly associated with *Helicina*) that will not be judged as to their final status, but they do show a similar embryonic shell structure, although much more strongly developed and have, in principle, the same arrangement of the female organs.

In *Helicina* s.s., the embryonic shell is very densely sculptured with large pits. The bursa copulatrix is the predominant accessory organ of the apical complex in the female reproductive system. It is complexly subdivided, whereas the provaginal sac appears simplified and much reduced. The ascending limb of the V-organ is elongated.

With respect to the above-mentioned characteristics the subgeneric units *Tristramia*, *Oxyrhombus*, *Pseudoligyra*, "*Cinctella*", *Succincta* and *Oligyra* were confirmed in their association with *Helicina*.

The species group "*Gemma*" *sensu* Wagner (1908) sharing shell characteristics with sub-

groups of *Alcadia* is now clearly distinguished from that genus and belongs to *Helicina* s.l.

Tamsiana, the second group in questionable position, could not finally be assessed in its relationship since adequate material was not available. A single embryonic shell studied (ZMB 103314) is partially eroded, and the surface can only be described with uncertainty as very scarcely pitted and crossed by very slight oblique lines. The figure of the female system given by Baker (1922a) shows a much reduced bursa copulatrix and a very large provaginal sac. Assuming the provaginal orifice to be incorrect, these characteristics would approach those of *Analcadia* and subordinate *Tamsiana* to *Helicina*, but a reexamination of the female system is still required.

The northern South American subunits *Analcadia* and *Sericea*, both studied by the respective type species, have to be rearranged from *Alcadia* to *Helicina*. They have a less densely pitted embryonic shell in common with a tinge of oblique lines and a strongly enlarged provaginal sac with a basal appendage. Furthermore, *Analcadia* and *Sericea* share the feature of a hairy periostracum, which is absent in other subgroups of *Helicina*. These similarities probably indicate a close relationship of both taxa, but, on account of the differently developed bursa copulatrix and the conspicuous sac on the middle portion of the pallial oviduct of *Helicina* (*Analcadia*) *dysoni*, the taxa are tentatively recognized as separate subgenera of *Helicina*.

Study of the Brazilian species "*Helicina*" *brasiliensis*, closely related to the type species of *Angulata* (*Helicina angulata*), shows a very different embryonic shell structure (broad, regular, concentric lines instead of pits or oblique grooves and radial threads), thus providing sufficient reason to raise *Angulata* to generic level. Older available names do not seem to exist. The anatomy of the female system resembles *Helicina* with respect to the bursa copulatrix, provaginal sac, receptaculum seminis, and the V-organ, but unfortunately the most important feature, the mon- or diallic condition could not properly be determined due to the poor preservation of the material available. Preliminary studies on other South American species suggest a higher diversity of the female system than in the Central American mainland species of *Helicina* and render the presence of a provaginal opening more likely than its absence. Beside the above-mentioned taxa *Tamsiana*, *Analcadia* and *Sericea* subgrouped

to *Helicina*, only four other supraspecific taxa have been based on South American species – *Angulata*, *Variabilis* Baker, 1922; *Concentrica* Baker, 1922; and *Trichohelicina*. *Variabilis* and *Trichohelicina* have not yet been investigated, the latter is discussed above under *Alcadia* (*Microalcadia*) n. subgen. Radula and female reproductive system of *Helicina concentrica* were studied by Baker (1923, 1926). Although the existence of a provaginal opening remains to be re-examined, the anatomical structures with a weakly lobed bursa copulatrix and a strongly enlarged provaginal sac show more similarities to the other species/ subgenera of northern South America (*Analcadia*, *Sericea*, *Tamsiana*) than to *Angulata*.

Because of the similarities of the female reproductive system of *Ceochasma* to *Helicina* and the absence of other distinguishing features, except for the outstanding and characteristic development of the deep slit-like sinus at the suture of the body whorl, the genus is hereby tentatively regarded as a subgenus of *Helicina*.

A subdivision of the Central American mainland species of *Helicina* remains difficult. The following available, non-synonymous supraspecific taxa (unless otherwise stated the synonymy given in Baker (1922a) for Central American mainland supraspecific taxa is accepted here) have to be considered: *Oligyra*, *Succincta*, *Tristramia*, *Oxyrhombus*, *Punctisulcata* and *Pseudoligyra*. The preoccupied "Formenkreis" names of Wagner *Gemma* and *Cinctella* were accepted by Baker (1922a) and type species were designated. Because Baker treated both as synonyms, differentiating features were never formulated.

As shown above, Baker (1926) could not find any anatomical characteristics distinguishing *Helicina* and *Oligyra*. Radula characteristics also do not contribute much to the differentiation of the taxa given above, for example, *Pseudoligyra* is said to differ from *Tristramia* only in the dentition of the C-central (4 cusps or rounded hook).

With respect to the Costa Rican species studied, two groups can be distinguished encompassing the following species:

1st group: *Helicina funcki*, *H. pitalensis*

2nd group: *Helicina beatrix*, *H. talamancensis*, *H. gemma*, *H. monteverdensis* n. sp., *H. chiquitica*

Remaining: *Helicina tenuis*, *H. escondida* n. sp., *H. echandiensis* n. sp., *H. punctisulcata cuericiensis* n. subsp.

The groups can be characterized as follows:

- 1st group: (a) embryonic shell: diameter of pits equal to interspaces, (b) surface structure of teleoconch with oblique diverging grooves, (c) cusps of marginal teeth slowly increasing in number, (d) provaginal sac irregularly lobed at distal side, (e) bursa copulatrix with numerous, often further subdivided lobes, central axis or lobes elongated, (f) males in volume a little more than 80% of females (in *Helicina pitalensis* not known).
- 2nd group: (a) embryonic shell: in some species diameter of pits smaller than interspaces and less densely pitted, (b) surface structure of teleoconch smooth, except for fine growth lines, (c) cusps of marginal teeth rapidly increasing in number and cusps more laterally arranged, (d) provaginal sac smooth at distal side, (e) bursa copulatrix with tendency to less numerous lobes, (f) males in volume about 62–70% of females.

Helicina tenuis, *H. echandiensis* n. sp. and *H. punctisulcata cuericiensis* n. subsp. fit in the first group except for (e) the rather simple bursa copulatrix and in (f) being intermediate between the groups with a male's volume about 75% of the female's (in *H. echandiensis* n. sp. only few individuals investigated, in *H. punctisulcata cuericiensis* n. subsp. unknown).

Helicina escondida n. sp. rather approaches the second group except for b) a surface structure similar to that of the 1st group although very slightly developed and in (f) being intermediate between the groups and equal to *H. tenuis* with a male's volume about 75% of the female's.

With respect to the radula, all the species have the common trait that at least the A-central is without well-defined cusps. Only occasionally it is crenulate or, in a single specimen, even denticulate, but not consistently for any species. Other deviations appear rather species-specific, for example, comb-lateral in *Helicina escondida* n. sp.

A comparison of the species investigated for the subgeneric units proposed by earlier authors (the type species of *Oligyra*, *Oxyrhombus*, *Pseudoligyra* and "*Gemma*", possibly related species for *Tristramia* and *Punctisulcata*, for *Succincta* and "*Cinctella*" only literature data were available) does not resolve clearly differentiated groups. At this level, the detailed embryonic shell structure does not seem to be applicable, because it already intergrades among the groups of the

Costa Rican species otherwise separated by different characteristics. For the female reproductive system, two main trends can be recognized in the relative development of the bursa copulatrix and the provaginal sac and its stalk, but intergrades can also be found among the Costa Rican species. On one hand, the bursa is relatively large and more complex in its structure, and the provaginal sac is long-stalked and irregularly lobed at its distal side or end. On the other hand, the bursa copulatrix is simply subdivided and more or less reduced in the number of lobes, and the provaginal sac is smooth and more distinct in its outline. The first trend is significantly found in *Tristramia* and *Oxyrhombus*, "*Cinctella*" and to a lesser extent also in *Punctisulcata* and *Pseudoligyra*, sharing also the teleoconch surface structure of oblique diverging grooves. This group most closely resembles *Helicina* s.s. from the West Indies. The other trend is developed in "*Gemma*" in combination with a very smooth shell. *Oligyra* and *Succincta* represent an intermediate stage, with a lobed provaginal sac and a remarkably reduced bursa copulatrix (although not to the same degree within different populations of *Helicina orbiculata*). Furthermore, they share the feature of an enlarged receptaculum seminis and a shell sculptured with spiral grooves. Additionally, at least *H. orbiculata* exhibits the pattern of oblique diverging grooves on the teleoconch. According to Baker (1928), *Helicina* (*Succincta*) *flavida* combines similar characteristics.

Data of Baker (1928) allow the interpolation of the degree of sexual dimorphism for *Helicina zephyrina* (to *Tristramia*) of about 82% (portion: male's of female's volume) resembling the 1st group of the Costa Rican species.

Summarizing, the features of the embryonic shell and female reproductive system are helpful on the generic level, rather than for differentiating within this group of species, although the latter characteristics show tendencies that are probably worth following up for other species. Except for the trends in the denticulation of the marginals, which seems to be more influenced by the specimen size, differences in the radula appear more subjective rather than objective, or they are limited to single species. Although in the data predominantly limited to Costa Rican species, a correlation of shell similarities and the degree of sexual dimorphism is obvious. This fact provides evidence that these characteris-

tics, especially the features of the shell, are useful in recognizing relationships at the subgeneric level when the assignment to the genus is also verified by other features.

Considering the practical taxonomical necessity of assigning the Central American mainland taxa to certain subgroups and since other subgenera of *Helicina* can be recognized properly, although final definitive differentiating characteristics could not be found, the proposed arrangement is tentative and follows the similarities outlined above. *Tristramia*, *Oxyrhombus*, *Pseudoligyra* and ?"Cinctella" (the latter not studied) are assumed to be synonymous including the 1st group of the Costa Rican species. The name *Tristramia* has priority. Furthermore, *Oligyra* and *Succincta* are regarded as synonymous with *Oligyra* being the older name, but *Oligyra* and *Tristramia* diverge from the group of "Gemma", which encompasses the 2nd group of the Costa Rican species. This name will tentatively be used for the separate subgenus, although it will have to be replaced in case this subdivision must be modified by additional data. Presently, the proposal of a new name seems inappropriate.

The well-defined differences between *Helicina* and *Alcadia* and other subgenera mentioned above, together with the uniformity among the species from the Central American mainland with respect to otherwise distinguishing features, suggest a much closer relationship within the mainland species than was previously assumed. The genus *Alcadia* has been shown to be absent from the Central American mainland and northern South America, except for the newly discovered small species *Alcadia* (*Microalcadia*) *hojarasca* and *A. (M.) boeckeleri*, which is distinguished from the *Alcadia* s.s. and examples investigated from other West Indian species by the peculiarities outlined in the description of the new subgenus. The presence of only a limited number of small-sized species of a genus on the mainland, as is here shown for *Alcadia*, is paralleled in the genus *Lucidella* and the new world Vianinae (according to the definition of Thompson, 1980; the subfamilial arrangement will not be discussed here) with their main radiation in the West Indies. In this case, only the species *L. lirata* and *L. midyetti* Richards, 1938, or *Pyrgodomus microdinus* and *P. simpsoni* respectively occur on the mainland. By way of contrast, *Helicina* represents the predominant genus on the mainland

and is spread over the West Indian Islands, although the exact distribution still remains subject to further studies. This is due to the previous confusion with *Alcadia* according to the characteristics of the post-embryonal shell and the operculum, upon which the only classification including species of the West Indian fauna had been based. But the species *Helicina platychila* from Dominica (Lesser Antilles), included as an example, and the type species *Helicina neritella* from Jamaica (Greater Antilles) clearly confirm the wider distribution.

Other Central American Mainland Genera

Due to insufficient material, the genus *Pyrgodomus* could not be examined for features of the female reproductive system, but the similarities in shell shape and surface structure, embryonic shell and radula confirm the close relationship to the Antillean genus *Eutrochatella*. Especially the size of the embryonic shell appears to be characteristically reduced in these genera compared with *Helicina* and *Alcadia*. The examination of the type species of *Eutrochatella* revealed monaulic conditions in the female reproductive system rendering a closer affinity to *Helicina* likely. Up to now there has been no evidence for assuming that the monaulic condition evolved more than once. The different embryonic shell structure of *Helicina* as well as the radula characteristics of *Eutrochatella* were discussed as being subject to convergent developments. Whether or not the differentiation of *Pyrgodomus* at the generic level is justified, depends on further investigations of the West Indian species and the final re-examination of the anatomy of *Pyrgodomus*. The traditional treatment is therefore tentatively maintained, although, according to the present data, the divergence from *Eutrochatella* probably does not exceed those differences of the mainland subgenera of *Lucidella* and *Alcadia* to their West Indian subunits.

The same applies to *Lucidella* as to *Pyrgodomus*, namely that the main portion of the species inhabits the West Indian Islands and only a few species, such as *Lucidella lirata*, occur on the mainland. Therefore, the discussion will be limited to the typical subgenus and *Perenna* based on the presently investigated species from Costa Rica. According to the system of Keen (1960), which is adopted here, two additional subgen-

era, *Poenia* and *Poeniella*, are established on a species from Jamaica or the Lesser Antilles respectively. The investigation of the female reproductive system of *Lucidella lirata* as well as of *L. aureola* required the corrections of important details given by Baker (1926, 1928). Therefore, it does not only confirm the affinities of *Perenna* to *Lucidella* but also allows the clear differentiation of the genus by peculiar characteristics of the female anatomy. *Lucidella* lacks the receptaculum seminis on the inner side of the descending limb of the V-organ, which bears apical swellings, but possesses an additional sac-like structure for sperm storage at the posterior portion of the pallial oviduct. In the absence of the receptaculum seminis and in the shortness of the provaginal duct, *Lucidella* resembles *Schasicheila*. The differences in the embryonic shell structure outlined by Thompson (1982) were confirmed and, as in other genera, are parallel in the anatomical features. Furthermore, the investigation of the internal shell structures showed the peculiar attachment of the right portion of the retractor muscle on the penultimate whorl and a comparable long axial cleft. As stated above, *Perenna*, although diverging in shell shape, generally agrees with *Lucidella*, s.s., with respect to embryonic shell and female system, but the bursa copulatrix is more closely associated with the stalk of the provaginal sac than directly with the reception chamber. Additionally, the posterior portion of the pallial oviduct is less inflated and internally folded, thus providing further reasons for retaining the subgeneric separation.

Finally, the genus *Schasicheila* does not occur in Costa Rica and seems to be limited to Mexico and Guatemala, but it is included here to take all Central American mainland genera of the Helicinidae into account. *Schasicheila* is characterized by several peculiarities of the postembryonic shell and operculum (summarized by Wagner, 1907–1911). Its radula does not diverge remarkably from the typical denticulated type of *Helicina*, for example. Concerning its anatomy, Baker (1926, 1928) recognized the genus as one of the most aberrant groups of Helicinidae. Reexamination of the type species confirmed all of Baker's observations, especially with respect to the diaulic condition of the female reproductive system. The embryonic shell structure and the internal shell structure added further distinguishing features.

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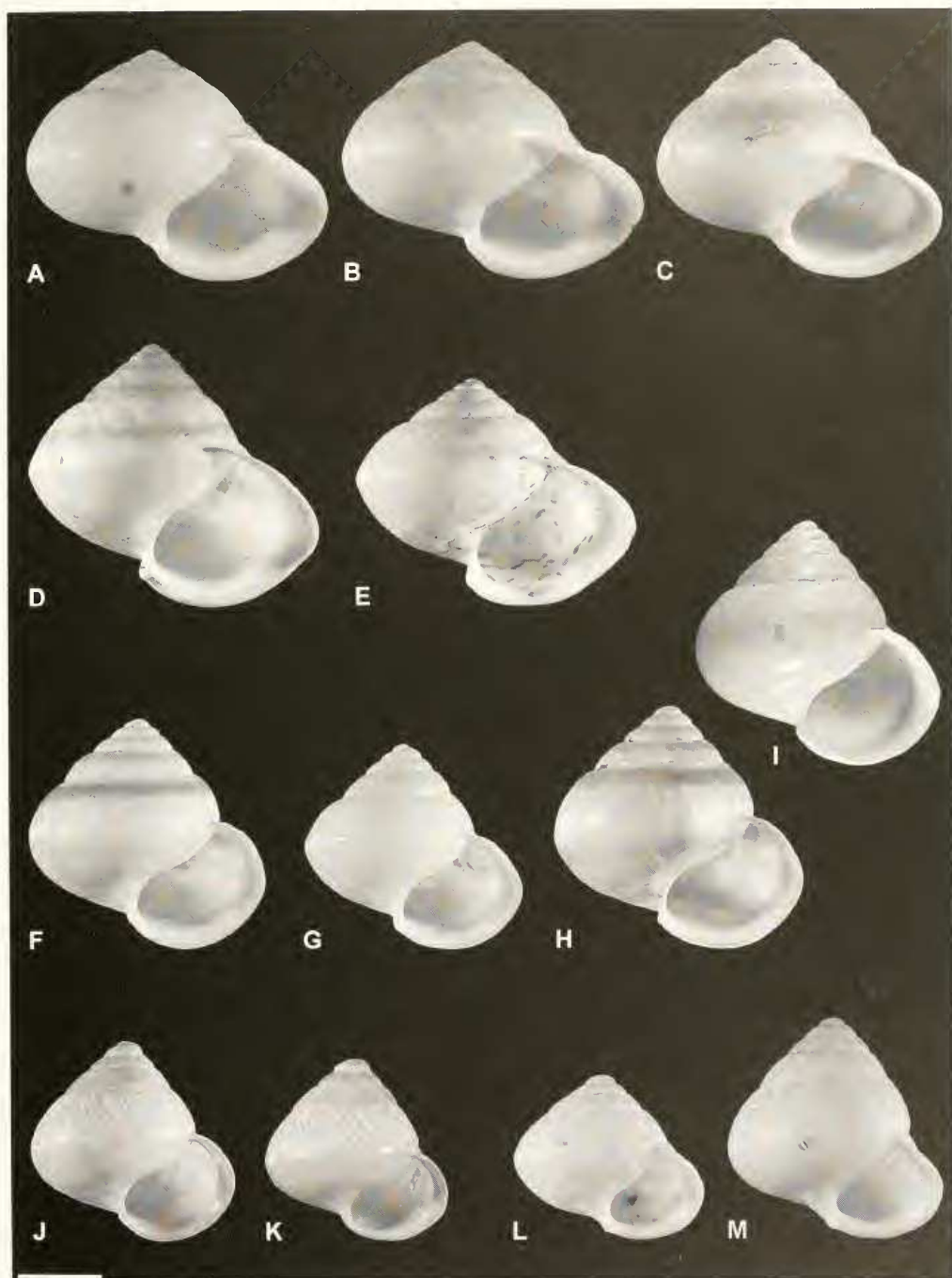


FIG. 335. A-C. *Helicina funcki*. A. Rio Barbilla. B. Manzanillo. C. Santa Elena. D-E. *H. pitalensis*. D. Bajo Bonito. E. Península de Osa. F-I. *H. tenuis*. F-H. Cabo Blanco. I. La Selva. J-K. *H. echandiensis* n. sp., campamento Echandi. L-M. *H. punctisulcata cuericiensis* n. ssp., Estación Cuerici; scale bars 4 mm (A-E), 3 mm (F-M).

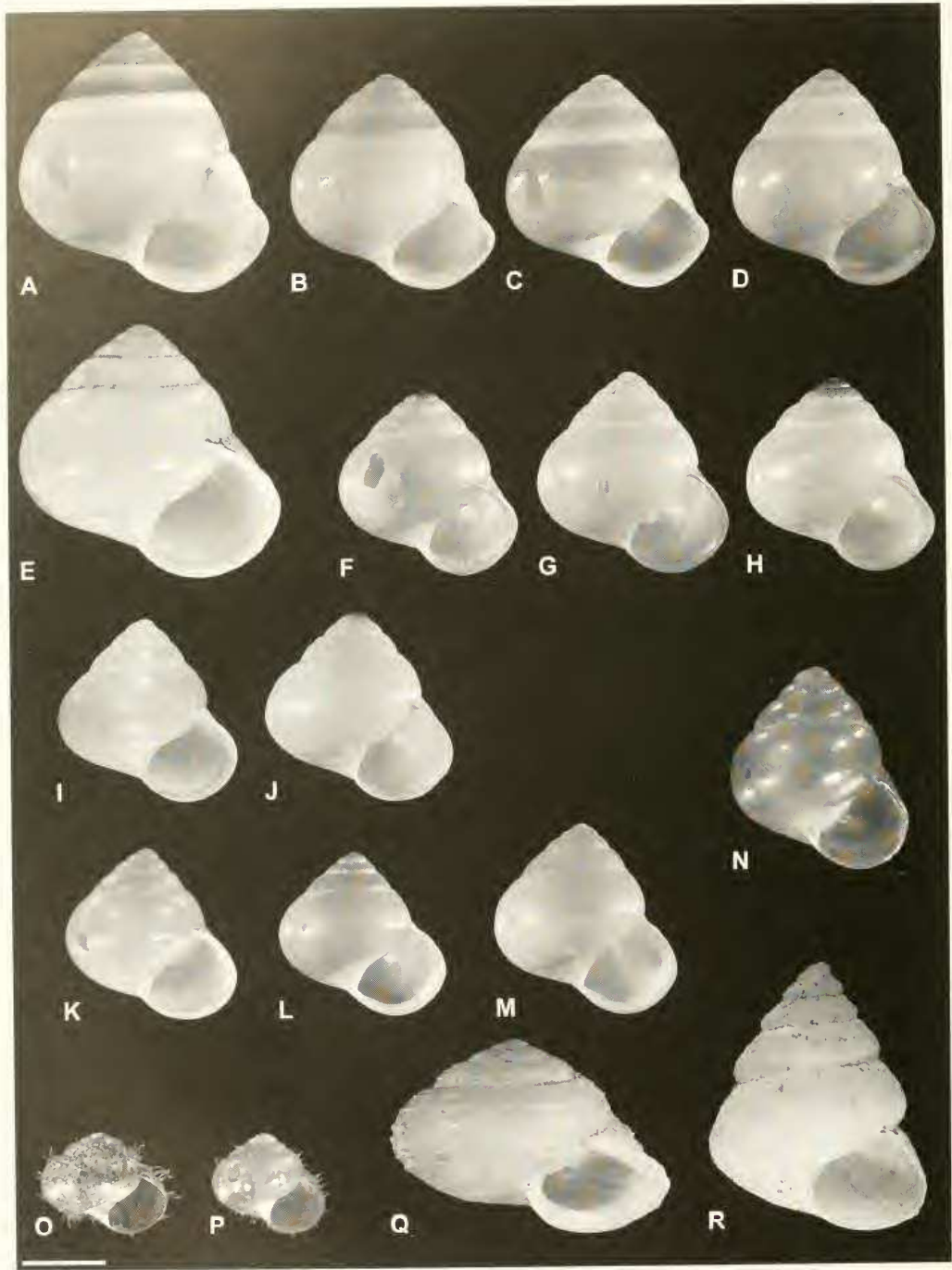


FIG. 336. A. *Helicina beatrix beatrix*, Guayacán. B-C. *H. b. confusa*. B. Uatsi. C. Shiroles. D. *H. b. riopejensis* n. ssp., Río Peje. E. *H. talamancensis*, Bajo Bonito. F-H. *H. gemma*. F. Cacao. G. Las Pavas. H. Siquirres. I-J. *H. montevertensis* n. sp., Monteverde. K-M. *H. escondida* n. sp., Río Barbilla. N. *H. chiquitica*, Río Barbilla. O. *Alcadia hojarasca*, Mirador Gerardo. P. *A. boeckeleri*, Pitilla. Q. *Lucidella lirata*, Cahuita. R. *Pyrgodomus microdinus*, Fila de Cal; scale bars 3 mm (A-M), 2 mm (N-P), 1.2 mm (Q-R).

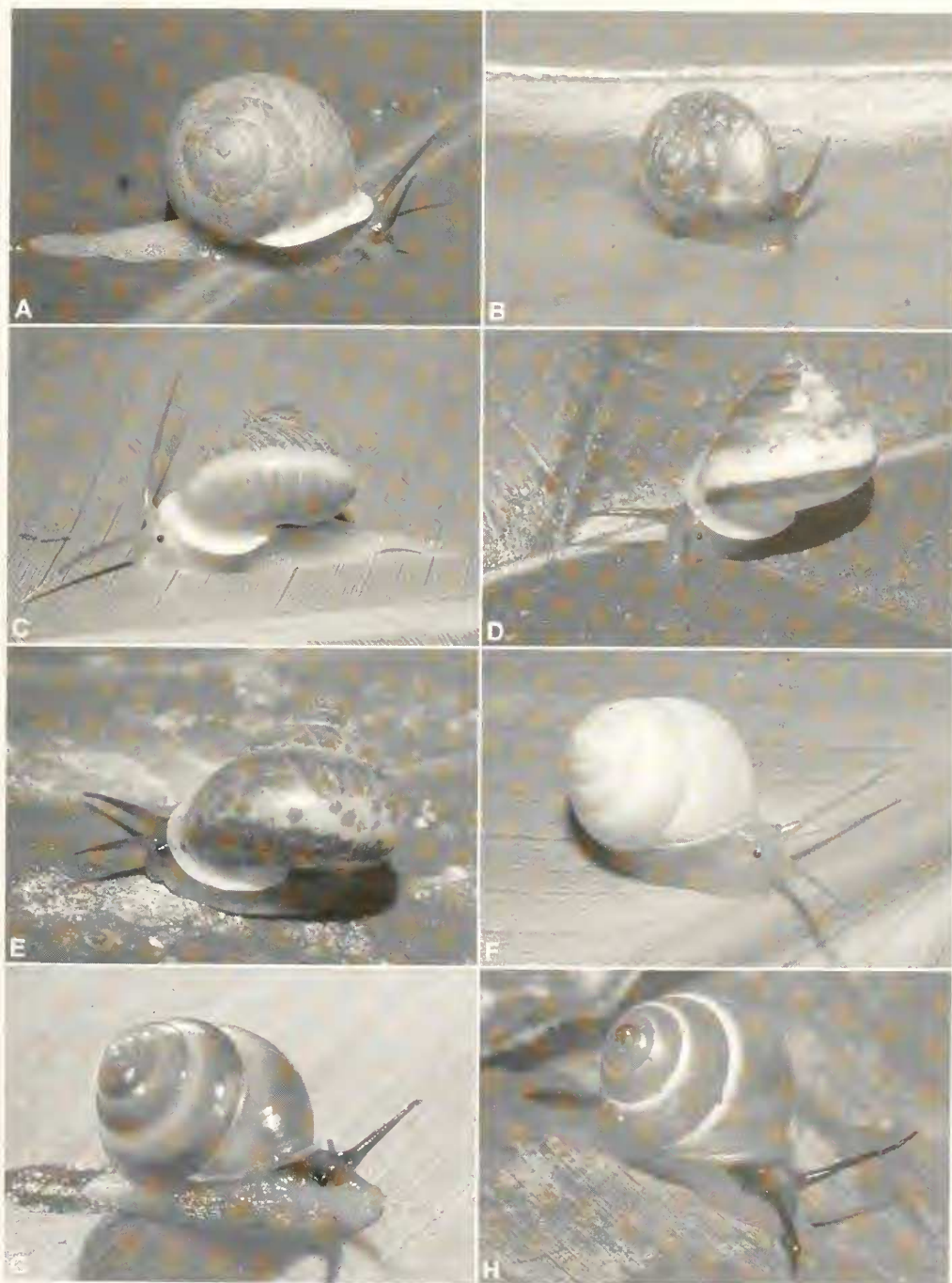


FIG. 337. Living animals of. A. *Helicina funcki*, Cahuita. B. *H. funcki*, juvenile, Uatsi. C. *H. pitalensis*, Bajo Bonito. D. *H. tenuis*, Cabo Blanco. E. *H. tenuis*, La Selva. F. *H. beatrix confusa*, Uatsi. G. *H. beatrix confusa*, Shiroles (photograph: V. Wiese). H. *H. beatrix riopejensis* n. ssp., Río Peje.

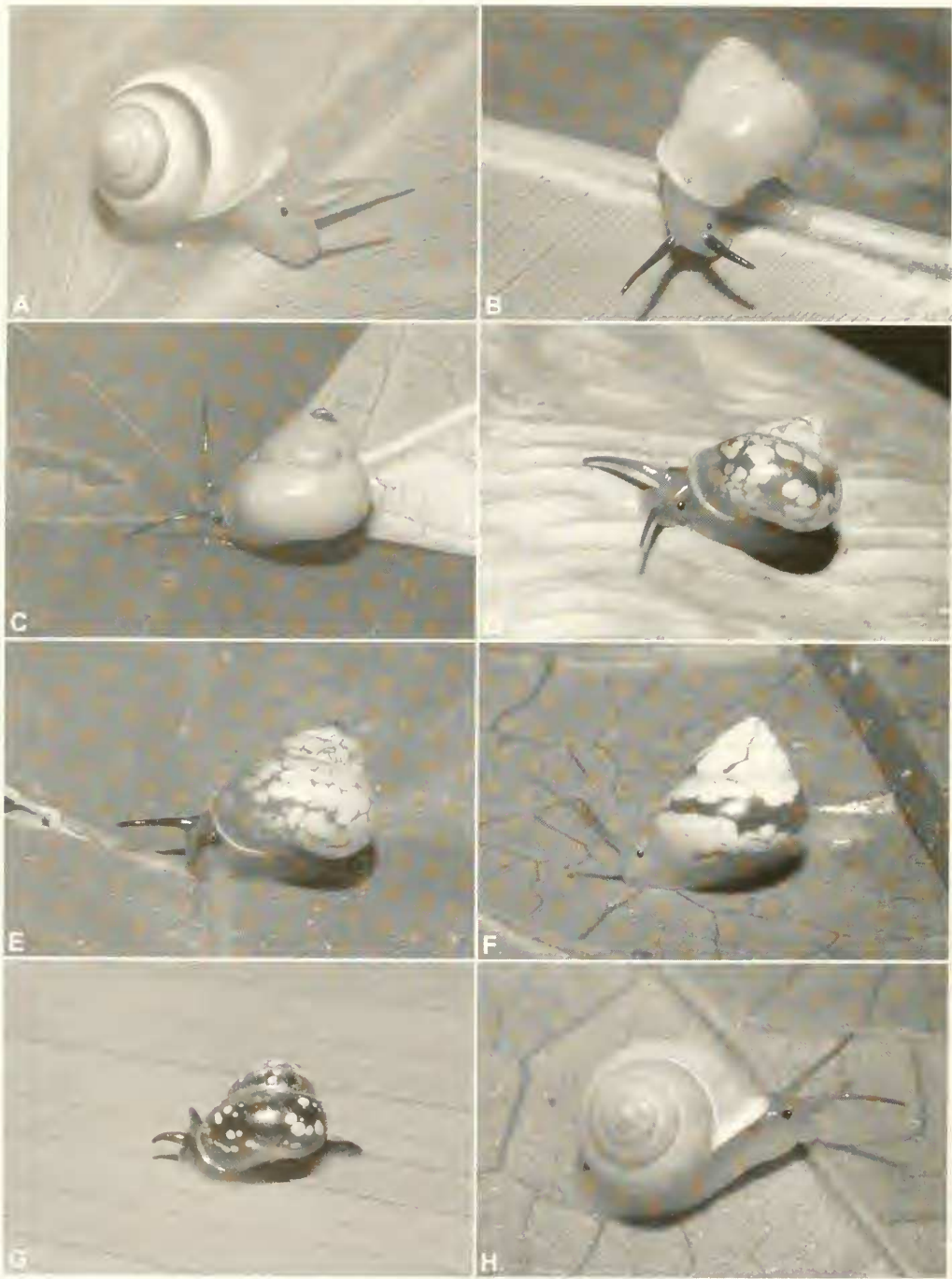


FIG. 338. Living animals. A. *Helicina beatrix beatrix*, Guayacán. B. *H. talamancensis*, Bajo Bonito. C. *H. gemma*, Cacao. D. *H. gemma*, Las Pavas. E. *H. gemma*, Siquirres. F. *H. monteverdensis* n. sp., Monteverde. G. *H. monteverdensis* n. sp., Mirador Gerardo. H. *H. escondida* n. sp., Shiroles.

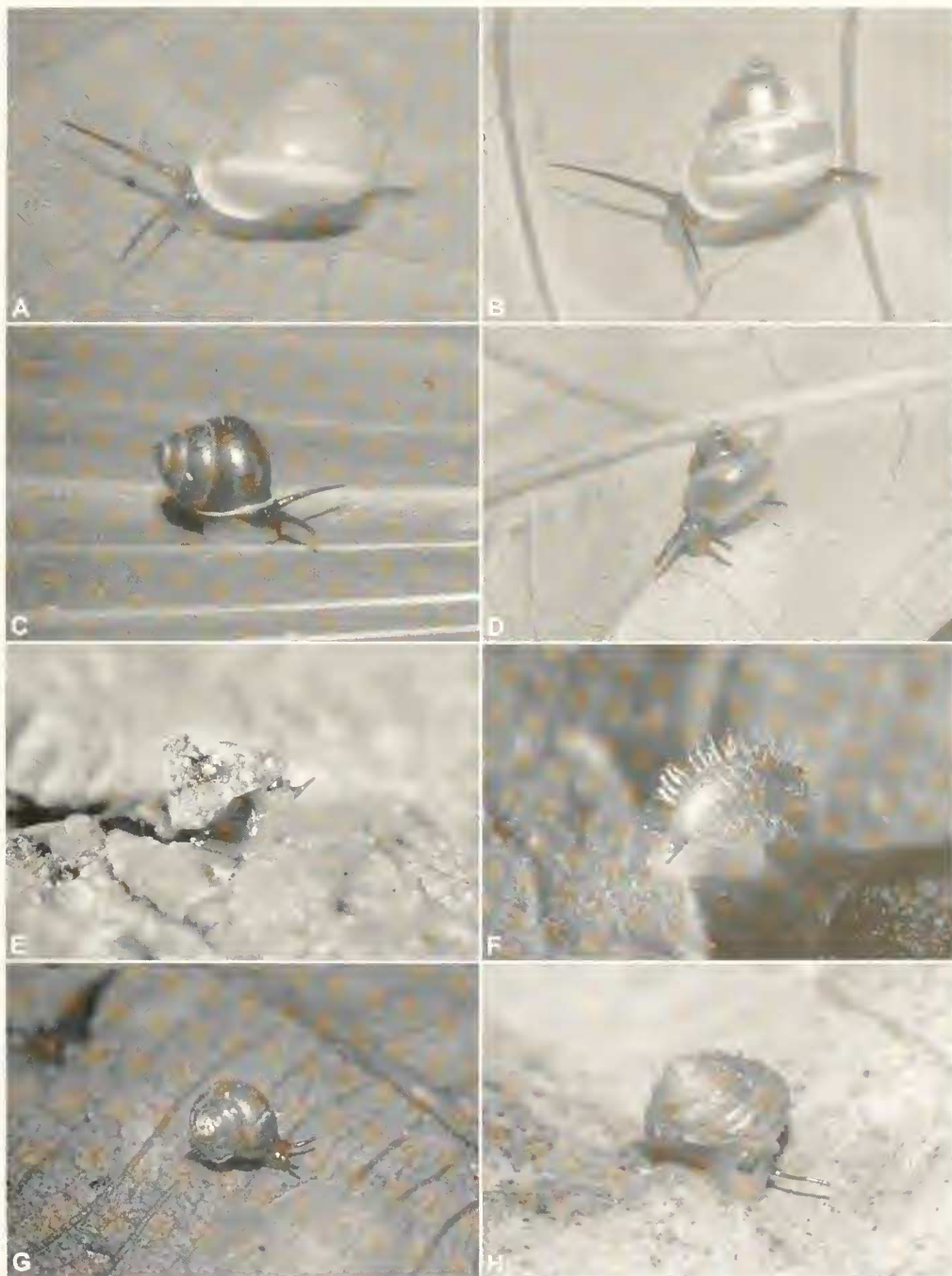


FIG. 339. Living animals. A. *Helicina escondida* n. sp., Shiroles. B. *H. escondida* n. sp., Rio Barbilla. C. *H. chiquitica*, Rio Barbilla. D. *H. chiquitica*, Rio Pacuarito. E. *Pyrgodomus microdinus*, Fila de Cal (photograph: V. Wiese). F. *Alcadia hojarasca*, Mirador Gerardo. G. *A. boeckeleri*, Pitilla. H. *Lucidella lirata*, Cahuita.

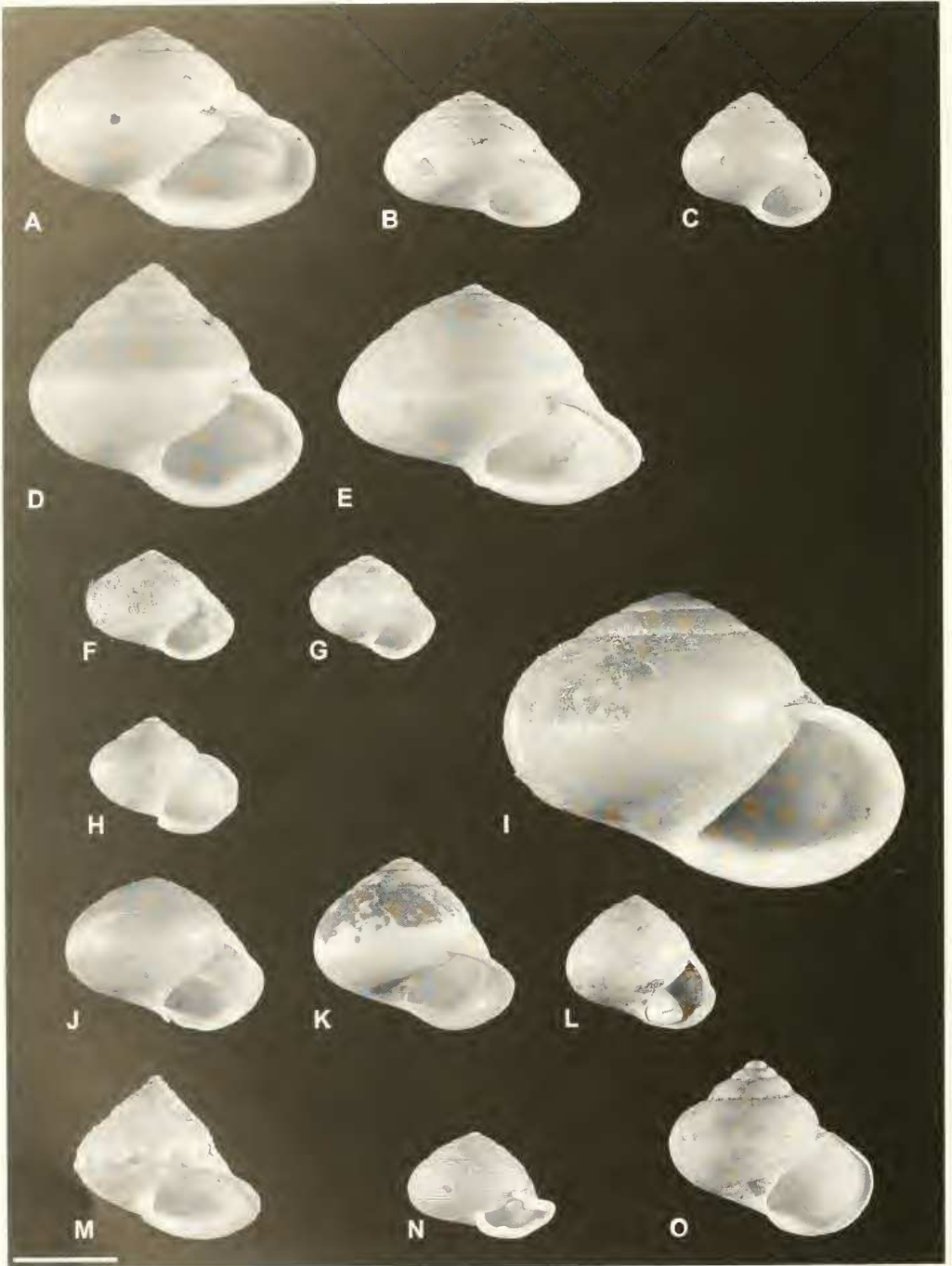


FIG. 340. A. *Helicina neritella*, Jamaica. B. *H. platychila*, Dominica. C. *H. orbiculata*, Florida. D. *H. turbinata*, Mexico. E. *H. amoena*, Guatemala. F. *H. dysoni*, Trinidad & Tobago. G. *H. sericea*, Suriname. H. *Angulata brasiliensis*, Brazil. I. *Alcadia major*, Jamaica. J. *A. hollandi*, Jamaica. K. *A. jamaicensis*, Jamaica. L. *A. rotunda*, Cuba. M. *Eutrochatella pulchella*, Jamaica. N. *Lucidella aureola*, Jamaica. O. *Schasicheila alata*, Mexico; scale bar 5 mm.

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